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New species of deep-sea gastropods from the Indo-West Pacific Region (Gastropoda: Vetigastropoda: Seguenzioidea: Calliotropidae) with a geologic and biogeographic perspective

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ABSTRACT

This paper identifies the biogeographic realm of Wallacea as a center of deep-sea (>200 m) endemism in the basal gastropod family Calliotropidae Hickman and McLean, 1990. Six new medium- to large-shelled species are described from Sulawesi: *Calliotropis bukabukaensis*, *C. tominiensis*, and *C.* new species from >1000 m in the Gulf of Tomini and *C. tabakuensis*, *C. locolocoensis*, and *C. lamuluensis* from the > 988 m in the Gulf of Bone. Two additional large-shelled species are described: *C. enantioserrata* from >1000 m on the eastern Australian slope in the northern Tasman Sea and *C. andamanensis* from 500 m in the Andaman Sea off the west coast of Thailand. Previous descriptions and records of *Calliotropis* species in Indonesia are from the margins of Wallacea—the Makassar Strait and Islands in the Banda Arc, notably Kai, Tanimbar, and Timor. When calliotropid biodiversity is connected with the large body of new knowledge of the contorted seafloor relief of the Indonesian region, it is clear that entire deep basins underlain by oceanic crust have never been sampled. The widespread occurrence of Cenozoic calliotropid gastropods in chemosynthetically based ecosystems is consistent with new data from petroleum exploration in the volcanic arcs of Indonesia documenting mud volcanoes and expulsion of geofluids (hydrocarbons, sulfides) that typically support rich microbial communities in the deep sea. The long and complex history of the collision of the Eurasian and Australian plates, arc volcanism, subduction, fusion of remnant pieces of continental crust, and opening of new deep gulfs affect the movement of shallow and deep currents and the Indonesian Throughflow from the Pacific into the Indian Ocean. This physical history generates testable hypotheses for reassessing the phylogenetic history of ancient gastropod lineages that originated in the Mesozoic Era or earlier.

Additional Keywords: Indonesia, Sulawesi, Wallacea, Indonesian Throughflow, plate collision, subduction, cold seep, chemosynthesis, intritacalx

INTRODUCTION

The Indo-West Pacific (IWP) region is recognized as the global center of marine biodiversity (Hoeksema, 2007; Bellwood et al., 2012). Efforts to understand patterns of elevated diversity of the invertebrate biota have centered on a triangular region (the Coral Triangle) identified in the literature by more than 15 different descriptive terms (see Hoeksema, 2007). This same region has long been famous as a terrestrial biodiversity hotspot encompassing the thousands of tropical islands of eastern Indonesia. In the marine realm, modern research has concentrated on characterizing and explaining tropical shallow marine diversity. In gastropods, this has included the use of molecular tools to document patterns of speciation and dispersal and to investigate genetic connectivity and species boundaries (Reid et al., 2006; Williams et al., 2011; Williams et al., 2012).

There is increasing evidence of a more localized deep-water hotspot for basal gastropod diversity in the region of Wallacea, in marine basins underlain by oceanic crust between the shallow continental shelves of the colliding Australian, Eurasian, and Philippine tectonic plates (Hickman, 2009a, 2009b, 2009c, 2012). Anatomical and molecular investigations of this putative deep hotspot are impeded by lack of deep-water sampling and access to fresh material. However, emerging geological, geophysical and hydrographic understanding of remnant deep basins and deep forearc settings provides an unparalleled opportunity to study closely correlated patterns in marine geology, geophysics, and biology.

The primary purpose of this paper is to describe new species of narrowly endemic basal marine calliotropid gastropods in the Indo-West Pacific Region. A preceding paper (Hickman, 2012) described a new genus and two new species in the trochoidean family Gazidae Hickman and McLean, 1990, and will be followed by an account of new species in the seguenzioidean family Cataegidae McLean and Quinn, 1987.

Secondary objectives are to offer some new perspectives on persistent problems and challenges of calliotropid systematics and to present new perspectives on the tectonics and complex geologic history of the assembly of Wallacea and the specific deep tectono-sedimentary settings in which the new species were collected.

There are >100 available names for putative living species of *Calliotropis* Seguenza, 1903. Some species are narrowly endemic, but others have unusually broad ranges in which disjunct populations may be separated by thousands of kilometers. There is no satisfactory basis for morphological delimitation of subgenera, and a conservative treatment of new species is adopted here pending revisionary systematics integrating shell, anatomical, and radular characters with molecular sequence data. Most species currently are known only from shells, but the amount of unstudied material in museum collections is substantial. There are excellent species-level accounts for the Indo-Pacific (e.g.,, Vilvens, 2004; 2006; 2007) and the Philippines (Poppe et al., 2006) that include detailed geographic and bathymetric range data. An important compilation of data on the taxonomy and distribution of 245 South African vetigastropod species (Herbert, 2015) lends weight to a previously subjective and perplexing disjunction of taxa between the South African and Indonesian regions. New data from Late Cenozoic fossil vetigastropods in the Philippines (Helwerda et al., 2014) add to a new baseline for revisionary work. The following brief account of the history of calliotropid systematics provides a framework and rationale for the descriptions of new species.

NOMENCLATURE AND CLASSIFICATION OF LIVING CALLIOTROPIDS

Calliotropid gastropods are known primarily from exploring expeditions beginning in the late 19th and early 20th centuries, notably the CHALLENGER, VALDIVIA, INVESTIGATOR, TRAVAILLEUR, TALISMAN, SIBOGA, PRINCESSE-ALICE, LIGHTNING, PORCUPINE, BLAKE, and ALBATROSS. Species were described or treated under a variety of genus-group names, including *Trochus* (*Margarita*) (e.g., Watson, 1879; P. Fischer, 1882), *Solariella* (e.g., Wood-Mason and Alcock, 1891; Smith, 1894; Locard, 1897; Sowerby III, 1903); *Basilissa* (e.g., Dautzenberg and Fischer, 1897; Martens and Thiele, 1904), and *Solarielliopsis* (Schepman, 1908). Names were based exclusively on shell features until Schepman (1908) observed and figured both shell and radula (reproduced here as Figures 1–2) noting "how dangerous it is to classify such species without any knowledge of the soft parts."

The nominotypical genus *Calliotropis* Seguenza, 1903 is based on a Pliocene-Pleistocene fossil species from Italy and is the name that has served for conservative treatments of more than 100 species from later deep-sea expeditions up until the present. Diagnosis of the family Calliotropidae Hickman and McLean, 1990 included features of the radula (Figures 3–4) that became clear with Scanning Electron Microscopy. They include a small-cusped "hooded" rachidian and large-cusped hooded lateral teeth with a system of deep interlocking basal projections and pockets, distinctive lateromarginal plates, extremely fine and numerous marginal teeth and peculiar mitten-shaped outermost marginal (Hickman

and McLean, 1990). An enlarged hindgut has been noted in many species along with evidence for selective deposit feeding (Hickman, 1981).

Other unique anatomical traits have been noted in calliotropids. The first is a large, enrolled, cylindrical elaboration of the right side of the male epipodium that has been interpreted as an "intromittent organ" (Dall, 1889) or "penis" or "copulatory organ" (Warén and Bouchet, 1989; Kano, 2007), or more conservatively as sperm delivery alternative to broadcast spawning that may not involve internal fertilization (Hickman, 1992; Kano, 2007). The second is the location of the "eyes" in some species at the bases of eyestalks and their modification to large irregular patches of black pigment (Dall, 1889). Observation of asymmetry and variability of the right and left pigmented regions has been interpreted as "a beginning of the loss of vision in an environment in which eyes are no longer of any use" (Warén and Bouchet, 1989). The asymmetry of the pigmented regions has been interpreted as evidence of separate genetic control of development of the right and left eye (Warén and Bouchet, 1989).

Twentieth century attempts to bring taxonomic order to *Calliotropis* include Marshall (1979) and Quinn (1979, 1991), although species have continued to be treated under inappropriate generic names (e.g., Abbott, 1974) or in inappropriate families (e.g., Nordsieck, 1968, 1982; Rubio and Rolan, 1987). A full review is beyond the scope of this paper.

Most significantly, the late 20th and early 21st century have seen a series of French deep-sea sampling expeditions recovering many calliotropids from bathyal depths in Oceania and the Indo-West Pacific Region. This work has further resulted in description of many new calliotropid species based exclusively on shell features (Poppe et al., 2006) and Vilvens, 2004, 2005, 2007) as well as new geographic and bathymetric records from the western Indian Ocean (Vilvens, 2006) and central Eastern Atlantic (Vilvens and Swinnen, 2008).

The monumental survey of Vilvens (2007) provides 251 figures of shells and classifies 94 species under *Calliotropis*, while declining to describe new subgenera or assign species to existing available genus-group names in the absence of anatomical data. Species are divided into 8 "formal groups" that are pragmatically justified and helpful for comparing shells of the same size and ratio of height to width. Descriptions and illustrations provide considerable additional detail such as numbers of cords on spire whorls and base, numbers of nodes or beads on spiral cords, whorl shape, and observations of ontogeny of these features.

Indonesia is the least well-sampled part of the Indo-Pacific Region. This is particularly unfortunate because it is geologically and hydrographically the most complex region on Earth and includes the Indonesian Throughflow (ITF) and the oceanic gateway connecting the Pacific and Indian Oceans (Tillinger, 2011). It is fortuitous that the Albatross Philippines Expedition of 1907–1910 included some exploratory deep dredging in
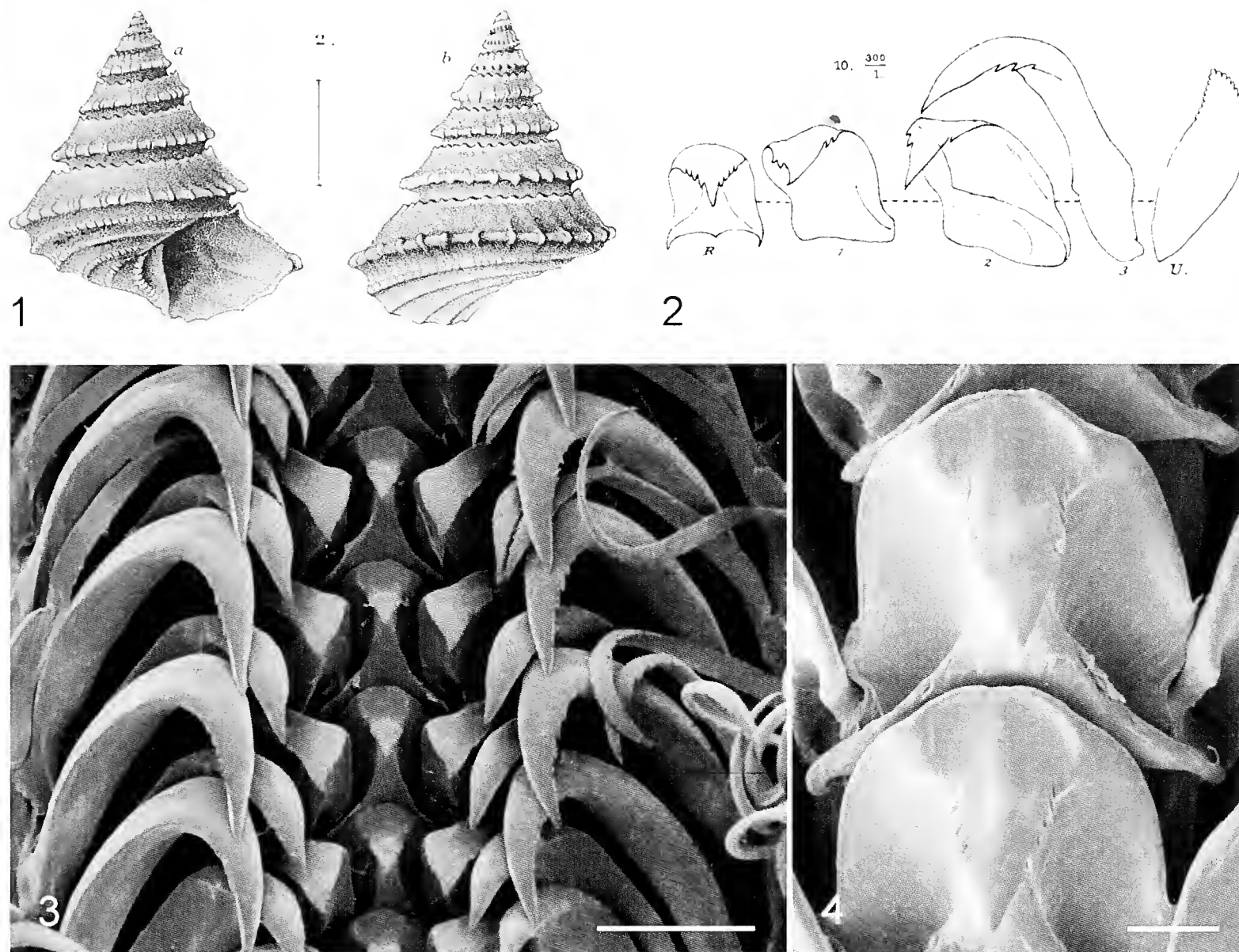
Figures 1–4. Calliotropid shell and radula. **1.** Schepman's original illustration of the shell of *Calliotropis pagodaformis*. **2.** Schepman's original drawing of the radula of *Calliotropis calcarata*. **3.** Scanning electron micrograph of the rachidian and lateral teeth from a typical calliotropid radula, scale bar = 100 μm. **4.** Detail of rachidian tooth cusp, shaft, hood and base, scale bar = 20 μm.

Indonesia (Sulawesi and Halmahera), and this paper documents six new calliotropid species from that expedition that have remained undescribed for >100 years. The paper also includes a new calliotropid species from the slope off eastern Australia and one from the eastern Andaman Sea.

NOMENCLATURE AND CLASSIFICATION OF
FOSSIL CALLIOTROPIDS

A full review of the treatment of the fossil record of this group is not directly relevant to the description of new living species. However, there is a long history of using separate family-group names for Mesozoic and Cenozoic lineages that differ little in shell morphology. Hickman and McLean recognized Eucyclidae Koken, 1897 as an extinct, primarily Mesozoic, family group with maximum diversity in shallow seas of the Jurassic and introduced the new family group name Calliotropidae (as Callio-

tropini) for the Cenozoic radiation into deep water of taxa previously classified under a variety of inappropriate trochoidean family-group names. During the last ten years, paleontological treatments have introduced new family-group names and reallocated both fossil and living genera (e.g., Bandel, 2010), or advocated the use *Calliotropis* sensu stricto for the Cenozoic forms and using *Riselloidea* Cossmann, 1909 as a temporal subgenus for the Mesozoic forms (Ferrari et al., 1014). This may seem to be a highly unsettled systematic state. However, recognition of the seguenzioid affinities of many Mesozoic and Cenozoic taxa (Warén et al., 2003; Bouchet and Rocroi, 2005) has revolutionized systematics. Equally revolutionary is the increasing molecular support for a deep divergence and common ancestor of hypothesized seguenzioid radiations (Kano, 2007; Kano et al., 2009; Aktipis and Giribet, 2012), including those into the deep sea. *Calliotropis* is effectively a form genus at this stage, but it is poised for an interesting revision integrating many kinds of data.

Successful revision will require new anatomical and molecular data and extensive taxon sampling. In terms of shell morphology, it will require consistent definition of characters in terms of clearly differentiated character states. Size and shape terms, measurements, ratios, angles, whorl counts, counts of sculptural elements are useful for defining ranges of variation within species represented by many specimens. However, their value is *descriptive* rather than *diagnostic*. Several untapped sources of morphological hypotheses of relationships are identified in the species descriptions that follow. They include the recognition of terminal growth in the form of a thickened or reflected outer lip, a descending aperture, and modes of complete or partial closure of an open umbilicus. A columellar denticle is a terminal growth feature, if it is not a continuation of a columellar plication or denticulation of the columella present in earlier columellar ontogeny. Little attention has been paid to shell microstructure and to modes of decreasing shell thickness. Nacre that is incompletely obscured by an unusually thin veneer of outer shell, and fine microsculptural features on the outer shell are potentially important for defining clades within Calliotropidae. They also are potentially useful for evaluating sister-group relationships of seguenzioidean families. For example, closely spaced wavy, irregular, and sometimes bifurcating axial microstructure on the adult shell is expressed in different patterns in at least three seguenzioid families. Micrographs for calliotropids are figured as "wavy threads" by Marshall (1979) and for chilodontids as "scratch-like marks" by Herbert (2012). They are expressed in a similar pattern on cataegids (personal observation). This peculiar microsculpture is typically accompanied by different patterns of infill or overprint by intritacalx deposits that have not been characterized. Chalky or flakey, partially calcified exterior layers on the shells of some gastropod and bivalve taxa (D'Attilio and Radwin, 1971) are a form of remote biomineralization (*sensu* Hickman, 2013). Intritacalx takes on new taxonomic potential in terms of the untested hypothesis that it is produced by sulfate-reducing microbes (Vermeij, 2014).

MATERIALS AND METHODS

Locality data are given as they were originally reported at the time of collection and recorded in their respective museum data bases. Indonesian place names for ALBATROSS specimens use spellings in the U.S. Fish Commission Oceanographic Data Set and data on the original specimen labels, followed by parenthetical current names, translations and spellings. ALBATROSS depths are reported in fathoms, as they were originally recorded, followed by parenthetical conversions to meters. Acronyms for specimen repositories are: AMS: Australian Museum, Sydney; ANSP: Academy of Natural Sciences of Drexel University (formerly the Academy of Natural Sciences of Philadelphia), Philadelphia; USNM: National

Museum of Natural History, Smithsonian Institution, Washington, DC.

SYSTEMATICS

Subclass Vetigastropoda Salvini-Plawen, 1980
Superfamily Seguenzioidea Verrill, 1884
(Eucycloidea Koken, 1897, unranked)
Family Calliotropidae Hickman and McLean, 1990

Genus *Calliotropis* Seguenza, 1903

Type Species: *Trochus ottoi* Philippi, 1844. Pliocene–Pleistocene, Italy, by original designation.

Calliotropis enantioserrata new species
(Figures 5–11)

Diagnosis: Shell conical, 8 whorls, large for genus (height >25 mm), height exceeding width (h/w = 1.2) conical, with straight-sided whorls and broad, smooth subsutural ramp between two sharply serrate spiral cords; suture impressed in deep channel between adapical spiral with abapically pointed serrations and abapical spiral, on succeeding whorl, with adapically pointed serrations; umbilicus completely closed by reflexed columellar callus; aperture prosocline at 43° to axis of coiling, not descending, but outer lip with prominent reflected terminal thickening.

Description: Exterior shell layer thin, ivory-colored, smooth, lacking periostracum or continuous intritacalx that covers shells of some large calliotropid species. Fine microstriations and intritacalx visible with magnification. Nacre clearly visible through translucent exterior layer and refracts green and pinkish iridescence. In addition to two serrate spiral cords on each spire whorl, a third faintly denticulate spiral present, covered by suture throughout growth. Five fine, faintly denticulate spirals on convex shell base. An interior oblique prismatic layer (sensu Gainey and Wise, 1975) apparently lacking, and nacre not extending onto terminally thickened and reflected apertural lip of adult. Protoconch (Figure 9) translucent, with one smooth whorl and distinct boundary with opaque and ornamented early teleoconch.

Flattened and broadly triangular serrations pointing in opposite directions on either side of sutural channel (Figure 10). Surfaces of tooth-like serrations finely striate under magnification (Figure 11), and brown intritacalx most prominently developed within sutural channel (Figures 10–11).

Remarks: The new species is superficially similar to *Calliotropis excelsior* Vilvens, 2004, which also has flat-sided spire whorls and a suture located in a deeply excavated channel bordered on either side by prominent serrate spirals cords. However, *C. excelsior* has an open umbilicus and lacks a terminally thickened apertural lip. It is restricted in distribution to Fiji and New Caledonia,
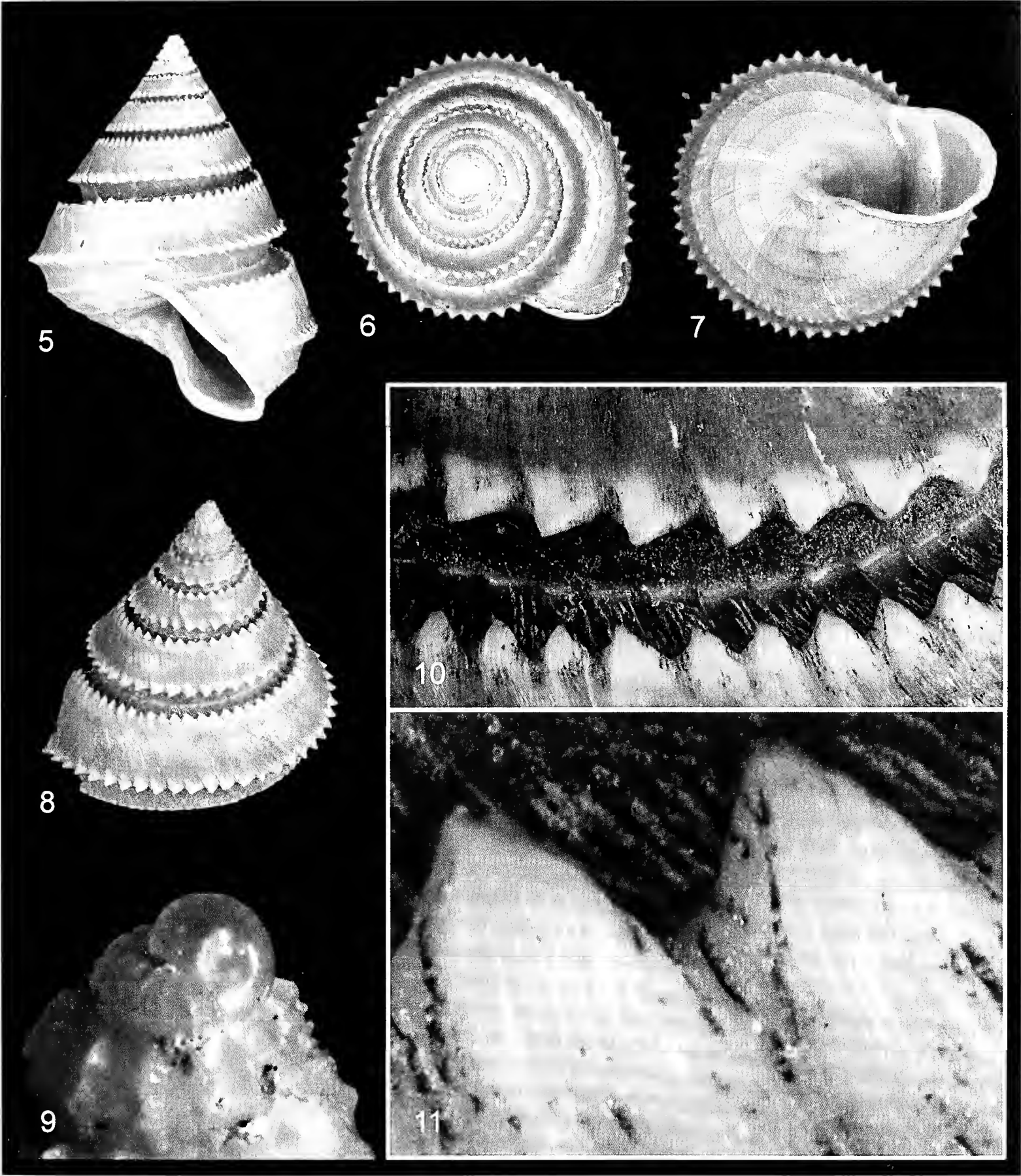
Figures 5–11. *Calliotropis enantioserrata* new species. **5.** Semi-apertural, **6.** Apical, and **7.** Basal views of holotype, AMS C152225, height = 29.6 mm. **8.** Inclined abapical view of the spire of paratype, AMS C142224, height = 15.8 mm. **9.** Detail of protoconch, from Figure 8. **10, 11.** Details from Figure 9 of sutural channel, bordering rows of serrations, microsculpture and intritacalx.

disjunct from the new Australian species. Shell proportions of the holotypes of the two species are identical, although all specimens of *C. excelsior* are smaller (height <25 mm).

The flattened and broadly triangular serrations pointing in opposite directions on either side of the sutural channel (Figure 10) are one of the most distinctive features of *C. enantioserrata*. The opposing direction of the serrations on the cords bordering the sutural channel is also shared with some specimens that have been assigned to *Calliotropis pagodaformis* (Schepman, 1908), a species first described from southeastern Indonesia with a range that subsequently has been extended to the Solomon Islands (Vilvens, 2007). The holotype of *C. pagodaformis* (Figure 2) is distinctive in its narrower width and higher spire as well as the concave spire profile giving it a classically pagodaform appearance.

Type Material: Holotype, AMS C152225; height, 29.6 mm, maximum width 24.0 mm, from type locality; Paratype: AMS C152224, height 15.8 mm, maximum width 14.7 mm, R/V Tongaroa Station U222, 32°49.3' S, 152°49.1' E, off Newcastle, 1040–1075 m, 9 October 1982.

Type Locality: R/V Tongaroa Station U223. 32°58.8' S, 152°41.6' E, off Newcastle, New South Wales, 951–1150 m, 9 October 1982.

Other Material Examined: AMS C152228; a single small, broken and worn specimen from R/V Tongaroa Station U223, the type locality.

Distribution: Known only from two stations off Newcastle, New South Wales, Australia.

Etymology: Greek *enantios* (opposing) + Latin *serrata* (toothed edge), referring to the saw-like appearance of the spiral cords on either side of the channel between whorls and the opposing direction in which the flattened tooth-like projections point.

Calliotropis andamanensis new species
(Figures 12–17)

Diagnosis: Shell conical, 8 whorls, moderately large (maximum height = 25 mm), width exceeding height (h/w = 0.92); spire profile straight-sided with three spiral cords; subsutural ramp broad and unornamented
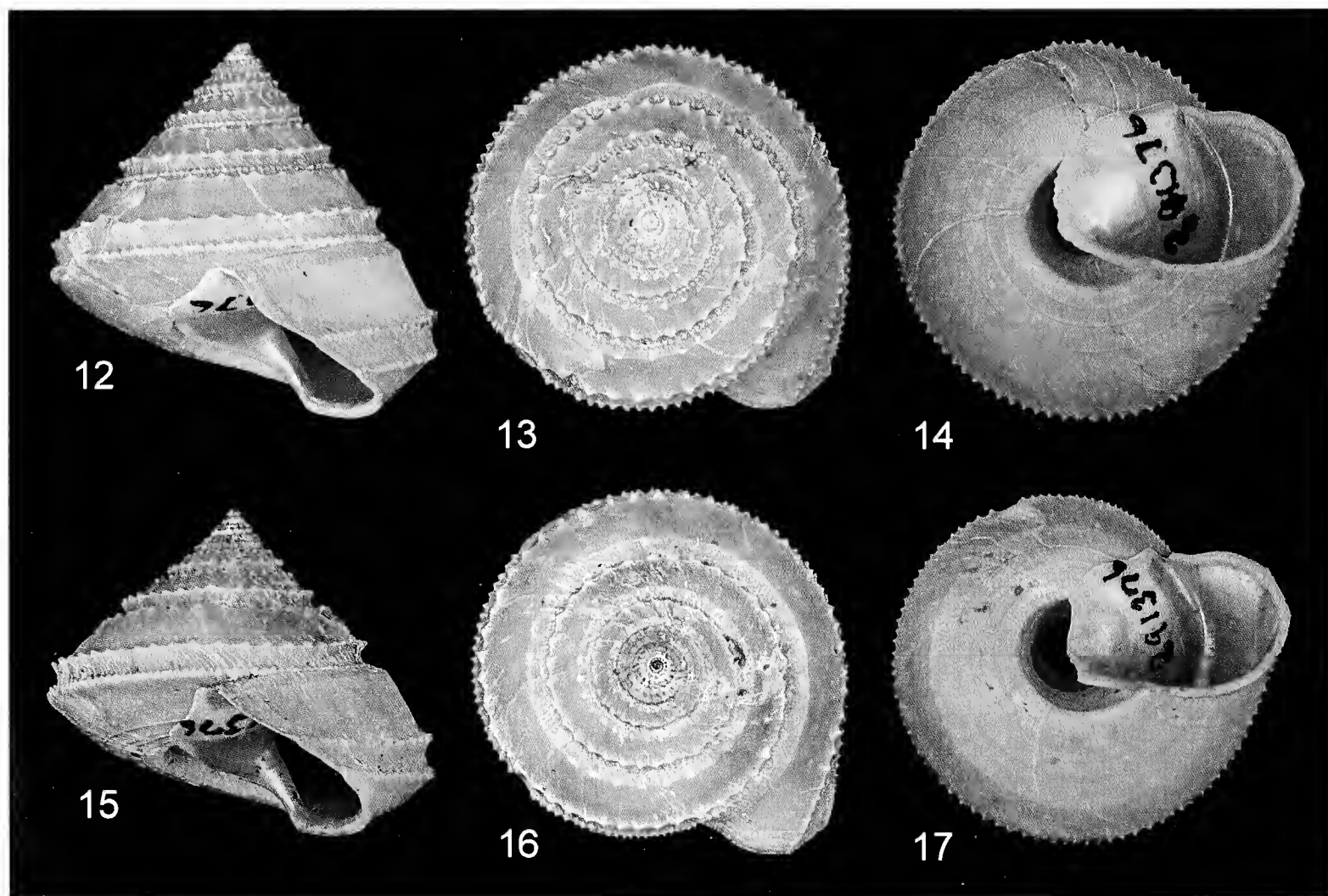
Figures 12–17. *Calliotropis andamanensis* new species. **12.** Semi-apertural, **13.** Apical, and **14.** Basal views of holotype, ANSP 291376, height = 25.0 mm. **15.** Semi-apertural, **16.** Apical, and **17.** Basal views of paratype, ANSP 465552, height = 21.2 mm.

between adapical spiral and closely spaced pair of sharply nodose spirals connected by closely spaced, strongly sinuous axial threads; nodes most prominent on middle spiral and weak but more numerous on abapical spiral; suture closely following third abapical spiral on spire whorls; aperture strongly descending on body whorl; terminal lip flared and reflected, but not strongly thickened; umbilicus broad and deep, partially covered by reflected projection of parietal and columellar callus.

Description: Outer shell layer very thin, lacking periostracum and intritacalx. Ivory-colored, with nacre visible as a predominantly greenish refractive luster. Base (Figures 14, 17) weakly convex and predominantly smooth, with four to six smooth to faintly nodose spirals bordering umbilicus. Nodes most prominent on spiral immediately bordering umbilicus. Sinuous axial threads increasingly visible between pair of abapical spirals (Figures 12, 15), consisting of uniquely distinctive feature of the species. Teleoconch whorls with microstriations but lacking intritacalx. Prominent callus deposit divided into non-nacreous reflexed thickening that is only partially covered by a smaller tongue of nacre over umbilical portion (Figures 14, 17).

Remarks: This species is superficially similar to the species in "Formal group 4" of Vilvens (2007), which includes relatively large shells in which width exceeds height. Some of the species in this group have a similarly robust development of parietal and columellar callus that either partially or fully covers a broad umbilicus. However, none of these species have a descending aperture (Figures 12, 15), and they differ in whorl profile as well as the number and ornamentation of spirals on the spire and base.

The distinctive features of *C. andamanensis* are consonant with its hydrographic isolation.

Although the Andaman Sea is in the Indian Ocean, it is geologically a deep Sundaland basin, separated tectonically from shallow Indian Ocean floor by the Sunda Trench. At the same time, it is topographically and hydrographically separated from Indonesia and the deep basins of Wallacea by the shallow Sunda shelf. There is no significant connection between Wallacea and the Andaman sea via the narrow and shallow Malacca Strait between Sumatra and Malaysia. The Indonesian Throughflow of Pacific water into the Indian Ocean (the largest movement of ocean water on Earth) is via the Makassar Strait between Sulawesi and Kalimantan, entering the Indian Ocean between Lombok and Bali and through the Timor Passage to join the west-flowing South Equatorial Current.

Type Material: Holotype: ANSP 291376, height 25.0 mm, maximum width 27.3 mm; Paratype: ANSP 465552, height 21.2 mm, maximum width 26.8 mm. Both from type locality.

Type Locality: R/V ANTON BRUUN International Indian Ocean Expedition, Cruise 1, Station 17, 07°40′ N, 97°08′ E, Andaman sea, off Phuket Island, Thailand, 503–512 m, green-brown clay, 1963.

Distribution: Known only from the type locality in the Andaman Sea off Phuket, west Thailand.

Etymology: Named for the type locality.

Calliotropis bukabukaensis new species
(Figures 18–22)

Diagnosis: Shell thin, conical, high-spired, and moderately large (height >15 mm), height exceeding width (height/width = 1.23); spire whorls stepped, with two sharply nodose spiral cords, suture impressed and slightly channeled above adapical spiral row of nodes; shoulder slope concave to slightly convex adapical to peripheral spiral cord with coarse nodes drawn out and connected; base with four thin, sharp spirals with concave interspaces ornamented with very fine axial lines; umbilicus broadly open, defined by finely beaded spiral and with fine axials on umbilical wall; columellar lip thickened and with prominent denticle extending into aperture.

Description: Nacre clearly visible through thin outer shell layer, remnants of thin, brownish-gold intritacalx present, best preserved on shell base and in umbilicus (Figures 20–22). Protoconch-teleoconch boundary not preserved on worn apex, but shell apparently with six or seven whorls. Aperture broken on all specimens, with no evidence of either thickened or descending apertural lip.

Umbilicus of holotype (Figure 20) partially blocked by thin, partially ruptured papery covering. This appears to have been formed by another organism, umbilicus of paratype (Figure 22) not similarly blocked.

Remarks: The new species is clearly distinguished from all previously described calliotropids by the very strongly developed, nodular columellar tooth (Figures 18, 21). Vilvens (2007) noted and illustrated (p. 42, figs 156, 158, and 160) a columellar tooth in three small-shelled species with depressed spires. In each of these species the denticle is considerably less well developed.

This is one of three new species recovered by the ALBATROSS in the Gulf of Tomini. It is easily distinguished from the large-shelled non-umbilicate species *C. tominiensis* and the smaller non-umbilicate *Calliotropis* new species?

Type Material: Holotype: USNM 239247, height 15.9 mm, maximum width 13.0 mm. Paratypes: USNM 1297170, height 12.5 mm, maximum width 11.3 mm; USNM 1409286, height 12.5 mm, maximum width 11.4 mm. All from type locality. Actual measurements are incomplete due to specimen breakages.

Type Locality: U.S. Fish Commission, R/V ALBATROSS, Station 5613, 00°42′00″ N, 122°44′00″ E, Gulf of Tomini,
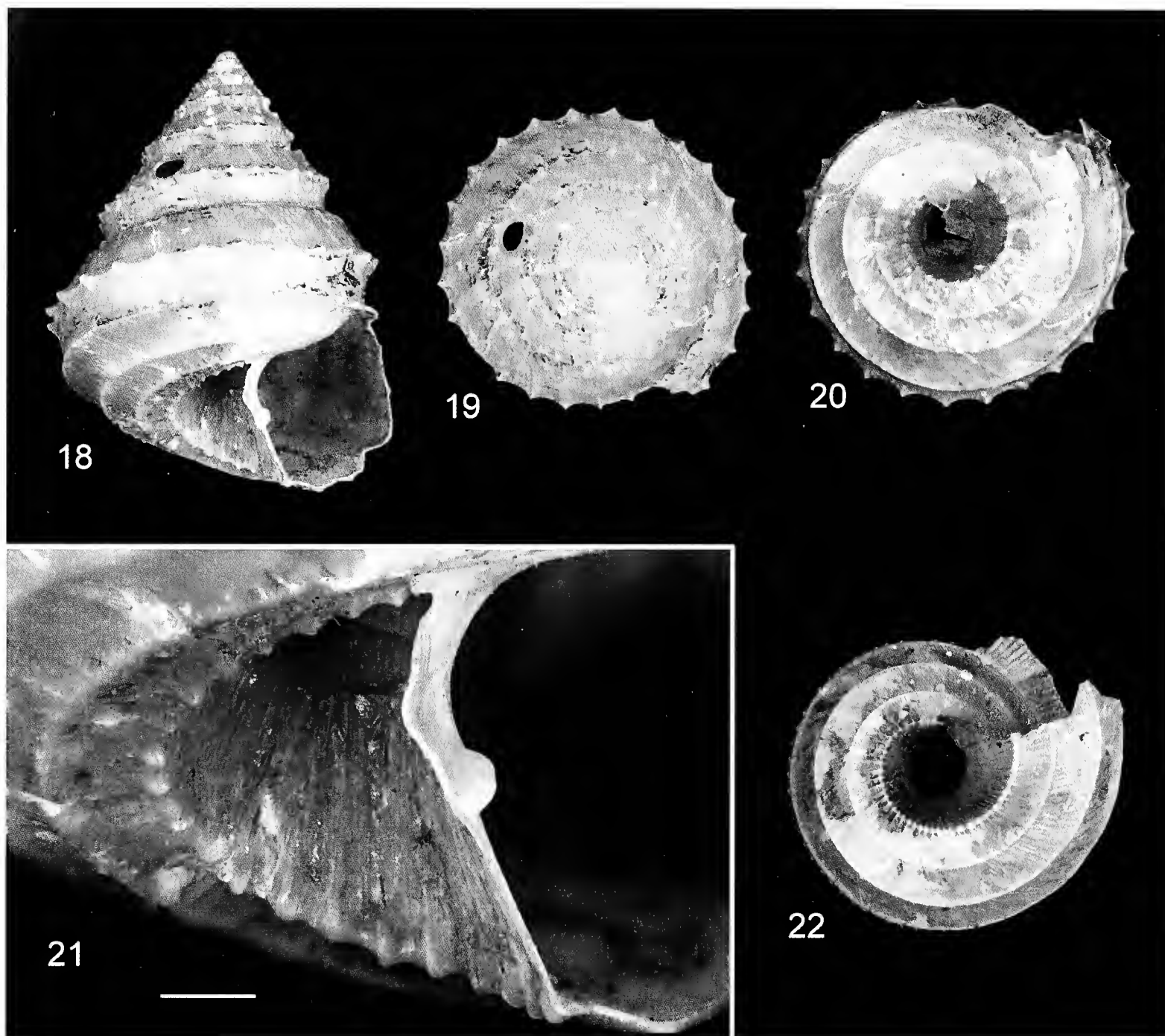
Figures 18–22. *Calliotropis bukabukaensis* new species. **18.** Apertural, **19.** Apical, and **20.** Basal views of holotype, USNM 239247, height = 15.9 mm. **21.** Detail of the columellar tooth and umbilical microsculpture of holotype, scale bar = 1 mm. **22.** Basal view of paratype with unoccluded umbilicus, USNM 1297170, height = 12.5 mm.

Celebes (Sulawesi), Togian Islands S. of Buka Buka Island, 752 Fathoms (=1375 m), gray mud, 20 November 1909.

Distribution: Known only from the type locality.

Etymology: Named for the type locality.

Calliotropis tominiensis new species
(Figures 23–25)

Diagnosis: Shell conical, 7 whorls, high-spired (spire angle = 58°, large (height >30 mm), height exceeding width (height/width = 1.31), spire whorls with one

prominent, nodose spiral cord; suture not impressed, closely following and almost completely covering second abapical spiral; base convex, with 4 finely beaded spiral cords; parietal and columellar callus reflexed, completely obscuring umbilicus and partially covering innermost basal spiral cord, aperture prosocline at 45° angle to axis of coiling; terminal lip thickened but not descending.

Description: Exterior shell layer extremely thin, with fine, closely spaced co-marginal lamellae and brownish-gold intritacalx well preserved on body whorl (Figure 23) and base (Figure 25). Outer layer eroded away on spire whorls (Figure 24) of holotype, exposing thicker nacreous layer that refracts predominantly green and pinkish
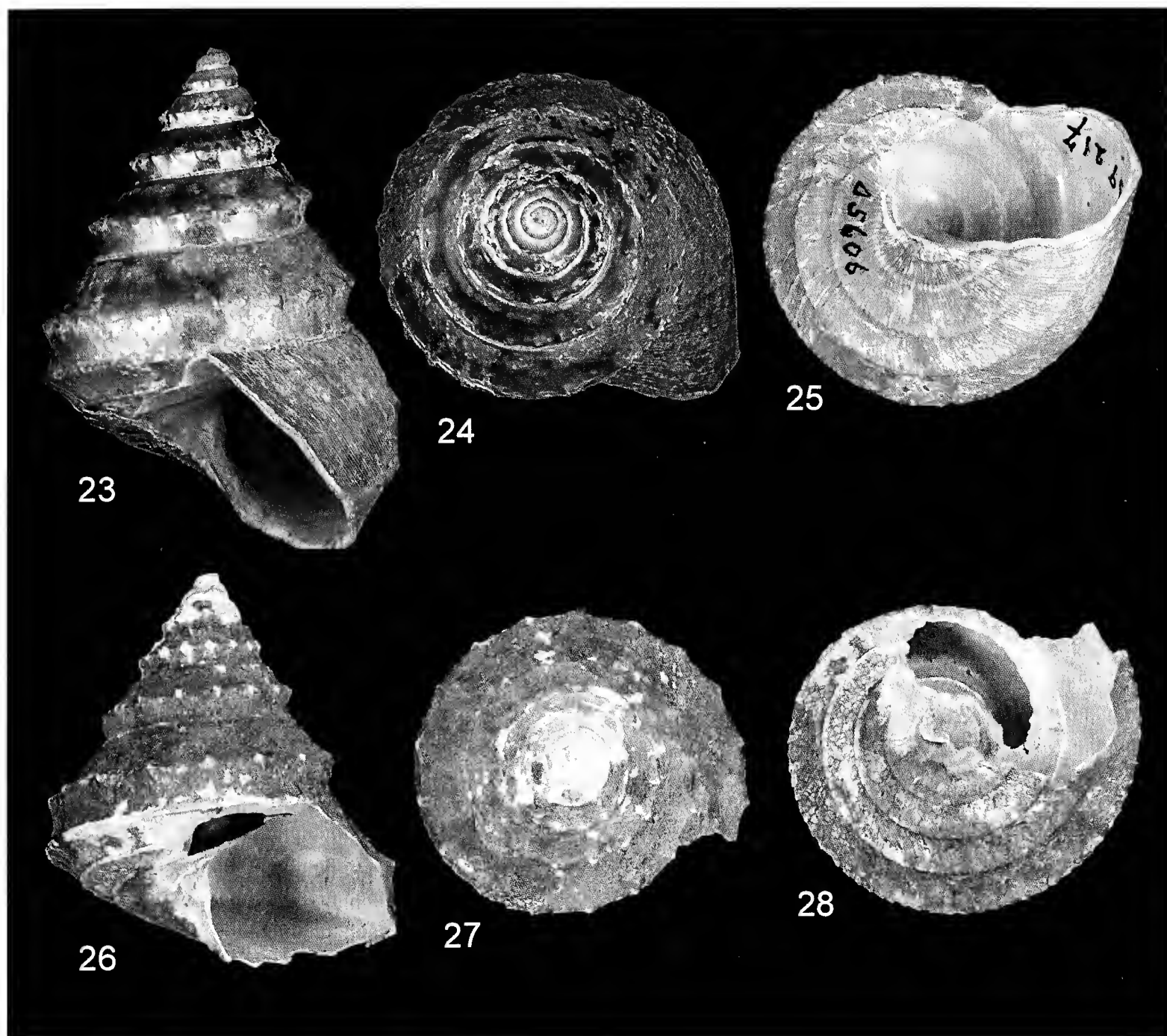
Figures 23–28. *Calliotropis tominiensis* new species and *C.* new species? **23.** semi-apertural, **24.** Apical, and **25.** Basal views of holotype of *C. tominiensis,* USNM 239217, height = 33.6 mm. **26.** Apertural, **27.** Apical and **28.** Basal views of figured specimen of *C.* new species, USNM 239216, height 15.7 mm.

iridescence (Figures 23–24). Inside aperture, nacre covered by very thin oblique prismatic layer that can be detected by touch—rougher toward interior and smoother toward apertural margin. Protoconch deeply eroded (Figure 24), and protoconch/teleoconch boundary not visible.

Remarks: There are very few species of *Calliotropis* that are as large and high-spired as *C. tominiensis. Calliotropis conocides* Vilvens, 2007, known only from the Solomon Islands, is similar in size and proportions (h/w of the largest paratype = 1.3). However, the Solomon species lacks the terminally thickened outer lip. It also lacks the extensive parietal and columellar

callus that covers the umbilicus of *C. tominiensis. Calliotropis cynce* Vilvens, 2007 from the Tanimbar Islands, in the Banda Arc of southeastern Indonesia, is less than half the height of the new species and has a less elevated spire (h/w ≤ 1.24). It also lacks the terminally thickened outer lip and extensive callus covering the umbilicus.

The biodiversity of the deep water basins of the Wallacean region of Indonesia is very poorly sampled, in contrast to the shallow waters of the region, which have been considered a crucible of species formation. Lack of sampling is unfortunate for two reasons. First, because of the megadiverse deep settings resulting from the complex and dynamic geological history of collisions, are

volcanism, subduction, suturing of continental fragments, post-collision extension to form new deep embayments, and the topographic barriers to migration. Secondly, because the region offers hydrographically and geologically unique opportunities to sample very great depths very close to shore in isolated embayments and adjacent to numerous small islands.

It is fortunate that the ALBATROSS spent a brief time in Indonesia at the end of the 1907–1910 Philippine Expedition, and material dredged from the Gulf of Tomini and Gulf of Bone in Sulawesi provides a unique window on calliotropid biodiversity in two unusual tectonic settings. The significance of these settings is considered in greater detail in the discussion section.

Holotype: USNM 239217, height 33.6 mm, maximum width 25.7 mm.

Type Locality: U.S. Fish Commission, R/V ALBATROSS, Station 5606, 00°16′28″ N, 121°33′30″ E, Gulf of Tomini, Celebes (Sulawesi), Togian Islands S. of Dodepo Id., 834 Fathoms (=1525 m), green mud, 17 November 1909.

Distribution: Known only from the type locality.

Etymology: Named for the type locality.

Calliotropis new species
(Figures 26–28)

Description and Remarks: An incomplete and worn shell recovered by the R/V ALBATROSS from >1000 meters in the Gulf of Tomini has a combination of characters that differentiate it from the five new Sulawesi species described herein. It is most similar to, and from the same station as, *C. tominiensis*. However, the peripheral spiral cord is prominently nodose and the shell is covered by an unusually heavy brown intritacalx with an exterior flaky layer in which there is imbedded sediment. The covering has adhered over most of the shell in spite of post-mortem corrosion and breakages (Figures 26–28). The spire angle is greater (67°), and the h/w ratio is less (1.1). The umbilicus is almost completely closed by parietal callus (Figure 28), and the columellar lip, which is not broken, is sharp rather than thickened and reflected as in the holotype of *C. tominiensis*. Additional material would be required to justify proposing a new name, and it is possible that the specimen is a juvenile of *C. tominiensis*. If umbilical closure is a terminal growth feature, this smaller specimen would have to be considered an adult.

Illustrated Specimen: USNM 239216, height 15.7 mm, maximum width 14.1 mm.

Locality: U.S. Fish Commission, R/V ALBATROSS, Station 5606, 00°16′28″ N, 121°33′30″ E, Gulf of Tomini, Celebes (Sulawesi), Togian Islands, S. of Dodepo Id., 834 Fathoms (=1525 m), green mud, 17 November 1909,

Calliotropis tabakaensis new species
(Figures 29–31)

Diagnosis: Shell conical, 7 whorls, large (height ≈ 17 mm), high spired (spire angle = 72°); spire moderately elevated with width and height almost equal (height/width = 0.9); spire whorls angularly convex, with two nodose spiral cords separated by concavity, suture shallowly impressed, following and barely covering fine, faintly beaded spire cord; adapical spiral on body whorl weaker with loss of nodes, peripheral spiral with 26 nodes; base weakly convex with four thin spirals that increase in width adapically, ornamented by slight swellings where crossed fine, sinuous axial threads; umbilicus open, aperture prosocline at 30° angle to axis of coiling; terminal lip thin and not descending.

Description: Protoconch of approximately one whorl, worn, boundary with teleoconch not clearly preserved (Figure 30). Outer shell layer thin, underlying nacre visible on entire shell surface. Intritacalx minimally developed and visible only under microscopic examination. Shell not encrusted during life or after death. Episodes of breakage and repair restricted to minor chipping of apertural lip.

Remarks: In size and proportions the shell fits in Formal group 4 of Vilvens (2007) and is superficially similar to *Calliotropis debriosa* Vilvens, 2004, a species known from 9 stations in the southwestern Pacific from New Caledonia to Fiji and at comparable depths. The new species is distinguished by its extremely thin shell, stepped appearance of the rounded whorls, open umbilicus, two prominent nodose cords on the spire whorls, and the nearly equal ratio of height to width.

This is one of three new species from the Gulf of Bone. It is remarkable that the linear distance separating the type locality of *C. tabakaensis*, off the western margin of the southeast arm, from that of *C. locolocoensis*, off the eastern margin of the south arm is only 50 km. However, the shelf on either side of the gulf is exceptionally narrow and drops off rapidly to depths of 2000 m in the center of the basin. The basin itself is subdivided into fault-bounded sub-basins, and study of the deep-water marine molluscan fauna merits further sampling with the geology and hydrography in mind. A feature of the Gulf that is especially pertinent to the occurrence of large-shelled calliotropid gastropods is the presence of hydrocarbon seeps (Camplin and Hall, 2014).

Holotype: USNM 239445, height = 17.3 mm, maximum width = 17.4 mm.

Type Locality: U.S. Fish Commission, R/V ALBATROSS, Station 5655, 03°34′10″ S, 120°50′30″ E, Gulf of Boni (Bone), Celebese (Sulawesi), Buapinang, 3 miles off Cape Tabaka (Tobaku). 608 Fathoms (= 1112 m), green mud and fine sand, 18 December 1909.

Distribution: Known only from the type locality.
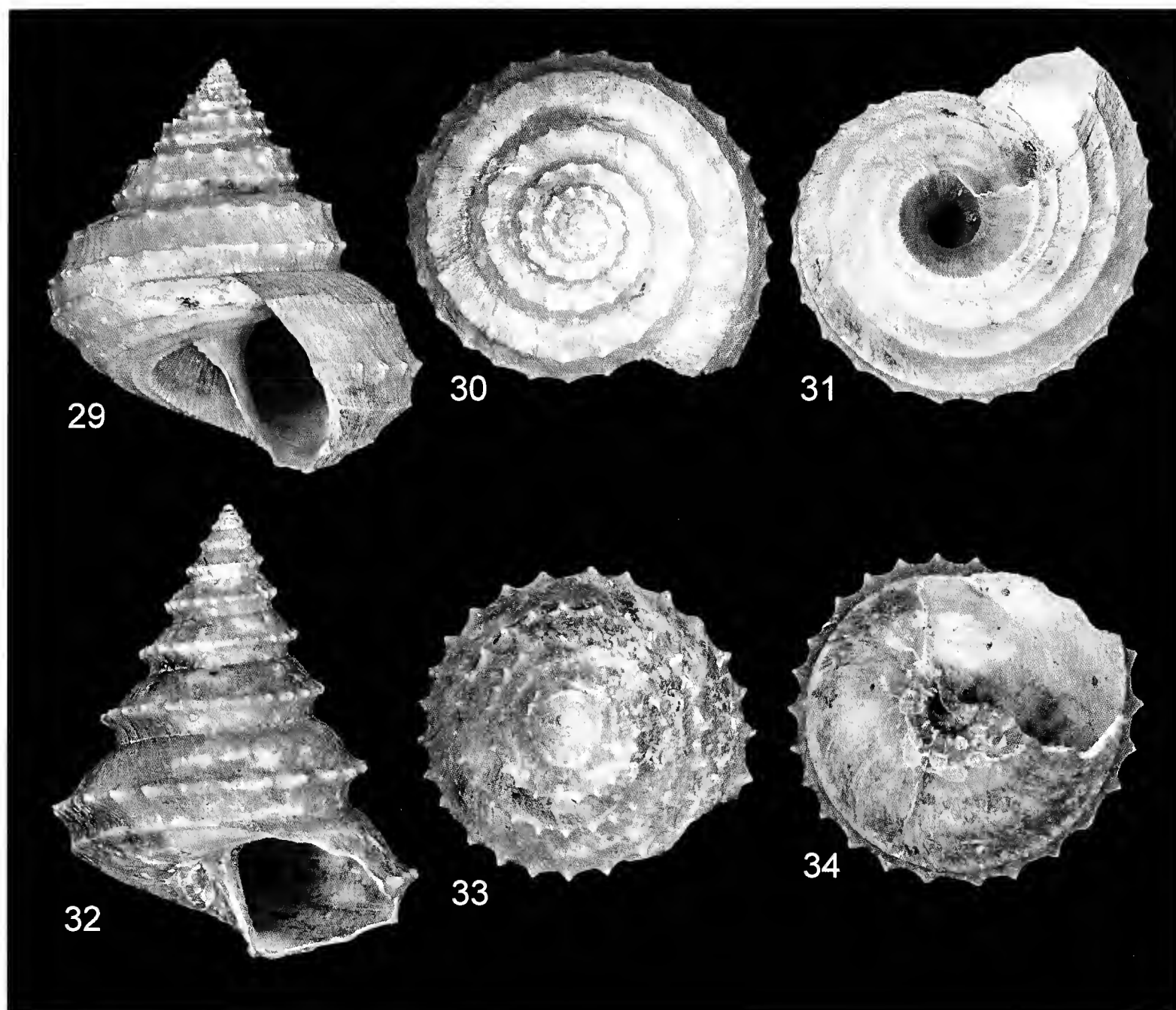
Figures 29–34. *Calliotropis tabakaensis* new species and *C. locolocoensis* new species. **29.** Semi-apertural, **30.** Apical and **31.** Basal views of holotype of *C. tabakaensis*, USNM 239445, height = 17.3 mm. **32.** Apertural, **33.** Apical and **34.** Basal views of holotype of *C. locolocoensis*, USNM 245478, height = 18.2 mm.

Etymology: Named for the type locality.

Calliotropis locolocoensis new species
(Figures 32–34)

Diagnosis: Shell conical, 9 whorls, unusually slender and high-spired (spire angle = 55°), large (height >15 mm), height exceeding width (height/width = 1.23); spire whorls with one bluntly spinose, keel-like spiral cord; base shallowly convex and smooth, bordered adapically by unornamented spiral; umbilicus almost completely covered by reflexed columellar and parietal callus and bordered by two faintly nodose spiral cords; outer shell layer covered by thin but continuous tan-colored intritacalx,

thicker inner nacreous layer visible through the outer shell layer where intritacalx has eroded away.

Description: Outer lip of holotype broken, but the trace of the break indicates that the final lip was not descending. Throughout ontogeny, it followed and covered the unornamented spiral defining the break between the spire and the base of the shell. The protoconch is approximately one whorl and worn so that the protoconch-teleoconch boundary is indistinct.

Remarks: In size and general appearance there is a close, but superficial, resemblance to *C. pagodaformis* (Schepman, 1908), originally described under *Solarielliopsis* Schepman, 1908 for inclusion of 11 deep-water

Indonesian species. Schepman based the genus on *S. calcarata* recognizing that his type species had a radula (Figure 2) distinct from that of *Solariella* Wood, 1842. Although he had no radular data for the other ten forms that he placed in *Solarielliopsis*, he emphasized (p. 53) "how dangerous it is to classify such species, without any knowledge of the soft parts."

Schepman's original figure of the shell of *C. pagodaformis* is reproduced above (Figure 1) for comparison with *C. locolocoensis*. The spire whorls of the new species have a single beaded spiral at the periphery and lack the subsutural spiral with adapically directed spines. The suture is not in a channel, and the shoulder slope is slightly convex rather than flat. The base lacks distinct spiral cords, and the columella is slightly prosocline rather than coincident with the axis of coiling.

There are prominent plate tectonic and hydrographic barriers separating the superficially similar pagodaform species in Indonesia. Schepman's localities from the Siboga Expedition were in the Outer Banda Arc thrust belt of eastern Indonesia, whereas the Albatross station is in deep water very close to shore in the Gulf of Bone in Sulawesi. The gulf is a complex, post-collision, extensional basin, emptying to the south into the Flores Sea. The gulf opened during the Neogene to separate the south and southeast arms of Sulawesi (Sudarmono, 2000; Camplin and Hall, 2014). Four Indonesian localities from which *C. pagodaformis* has been collected more recently (March, 1990) and reported by Vilvens (2007, p. 7) are also in the Banda Arc (Tanimbar Islands), tectonically in the collision zone between the Australian continental margin and the Banda volcanic Arc above the Timor trough (Barber et al, 1986). The three new species described here from the Gulf of Bone may reflect its isolation and separate geologic history.

Holotype: USNM 245478. Height 18.2 mm, maximum width 14.8 mm.

Type Locality: U.S. Fish Commission, R/V ALBATROSS, Station 5658, 03°32′40″ S, 120°31′30″ E, Gulf of Boni (Bone), Celebes (Sulawesi), off Loko Loko (Locoloco), 510 Fms. (=933 m), gray mud, 19 December 1909.

Distribution: Known only from the type locality.

Etymology: Named for the type locality.

***Calliotropis lamuluensis* new species**
(Figures 35–37)

Figures 35–40. *Calliotropis lamuluesis* new species and *C. glypta* (Watson, 1879). **35.** Semi-apertural, **36.** Apical and **37.** Basal views of holotype of *C. lamuluensis*, USNM 239424, height = 19.4 mm. **38.** Semi-apertural, **39.** Apical and **40.** Basal views of a hypotype of *C. glypta*, AMS C.115685, height = 17.2 mm.

Diagnosis: Shell broadly conical, 6 whorls, low spired (spire angle = 90°, large (height ≈ 20 mm), width exceeding height (height/width = 0.84); spire whorls weakly convex, with two (increasing by intercalation to three) nodose spiral cords; suture shallowly impressed beneath and following abapical spiral; body whorl with three coarsely nodose spirals on shoulder slope (30, 34 and 38 nodes from adapical to abapical spiral on body whorl), peripheral spiral more finely nodose (65 nodes on body whorl); base weakly convex with seven sharply nodose spirals that become increasingly wide and more distinctively nodose abapically; parietal and columellar callus strongly reflected and completely covering umbilicus; aperture strongly prosocline at 43° angle to axis of coiling, terminal lip very slightly thickened but not descending.

Description: Apertural lip of holotype chipped, four roughly circular attachments scars (Figure 36) present on body whorl made by an epizoan no longer present. Two major and several minor episodes of shell breakage and repair during growth. Periostracum not present. Fine, sinuous and prosocline axial "scratch-marks" on shell interspersed with minimally developed intritacalx. Protoconch and earliest portion of teleoconch broken, nacre visible in several places where very thin exterior shell layer is broken or eroded away. Nacre in interior of aperture covered, but visible through a thin oblique prismatic layer that is a characteristic feature of many large calliotropid shells. Nacreous layer in this species thicker than in most large calliotropids, giving shell a more robust appearance.

Remarks: *Calliotropis lamuluensis* differs dramatically in shell thickness, proportions, and many discrete features from the two new species described from farther within the gulf. As noted above, this may reflect isolation tied to the complex tectonic history and opening of the gulf (Sudarmono, 2000; Camplin and Hall, 2014). In view of the complex geology and hydrography and the hydrocarbon seepage reported in the Gulf (discussed above) these locations would profit from further sampling of the deep-water marine molluscan fauna.

The new species is closest in size, proportions, and ornamentation to the species in Formal group 4 of Vilvens (2007). It has the lowest h/w ratio of any of the species in the group and differs from these openly umbilicate shells in having a fully reflexed umbilical closure (Figure 37). It also differs from group 4 species in having a thicker shell. An Australian specimen of *Calliotropis glypta* (Watson, 1879), is illustrated here for comparison (Figures 38–40). Thickness of the basal portion of the apertural lip is 0.4 mm, in contrast to 0.7 mm for *C. lamuluensis*. Shells of both species supported encrusting epizoans to a greater extent than typical in other calliotropids.
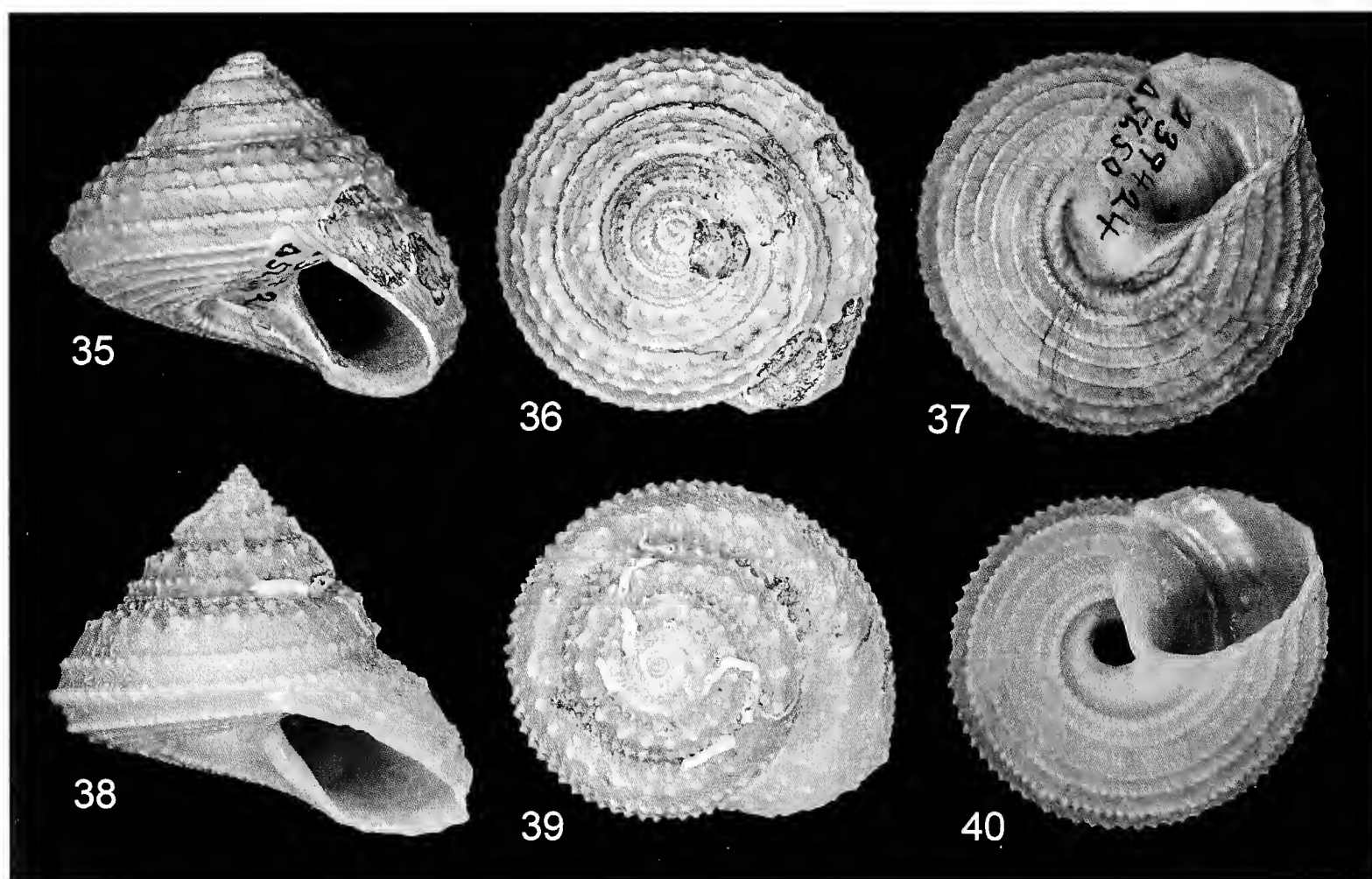
Holotype: USNM 239424, height = 19.4 mm, maximum width = 23.1 mm.

Type Locality: U.S. Fish Commission, R/V ALBATROSS, Station 5650, 4°53′45″ S, 121°29′00″ E, Gulf of Boni (Bone), Celebese (Sulawesi), Buapinang, off Lamulu Point, 540 Fathoms (=988 m), green mud, 17 December 1909.

Distribution: Known only from the type locality.

Etymology: Named for the type locality.

DISCUSSION

The new species described above shift the center of diversity of large-shelled (height > 15 mm) calliotropids into the tectonically and hydrographically complex Wallacean region of Indonesia, with its long history of plate collisions, subduction, and volcanic arc volcanism. They also shift peak diversity of large-shelled calliotropids to depths exceeding 1000 m. This is remarkable because the deep-water fauna of Indonesia is still undersampled. A previous paper (Hickman, 2012) provides additional background on the unique ecologic, biogeographic, and geologic aspects of Wallacean deep diversity.

A simplified map of deep Wallacea (Figure 41) shows the localities of the species described above and provides a frame of reference for the following discussion of patterns of narrow endemism, disjunction, and relictual accumulation of taxa.

The calliotropid species are spatially distributed in geologic settings that include tectonically isolated deep-water basins underlain by oceanic crust. In one interpretation (Lee and McCabe, 1986) the Sulu, Celebese, and Banda seas are characterized as remnants of a large Cretaceous–Eocene seaway. Tectonic elements of Wallacea include major forearc subduction complexes, fusions of colliding microplates, shifting plate boundaries, and formation of narrow gulfs and extensional basins opening by rollback at subduction hinges. The Molucca Sea is unique—the only modern example of double subduction at the collision of two facing volcanic arcs, eliminating an entire oceanic plate and trapped Indian Ocean lithosphere (McCaffrey et al., 1980; Hall, 2006; Hall and Smyth, 2008). This is the first recognition of the relictual deep-water fauna in a setting that has heretofore been of intense interest only to geologists.

The corresponding sedimentary and geochemical settings associated with the complex geologic history of marine Wallacea are consistent with the development of unusual deep marine communities. Convergent plate margins frequently are sites of expulsion of squeezed percolating fluids containing sulfides and hydrocarbons (oil, gas, and methane hydrates). These fluids feed microbial productivity and development of chemosymbiotically based food chains. Although such settings are typically not good candidates for the formation of large petroleum reservoirs, ongoing investigations of petroleum potential in Indonesia have revealed the presence of discrete hydrocarbon seeps, mud volcanoes and explosive methane release (Barber et al., 2000; Sudarmono, 2000; Charlton,
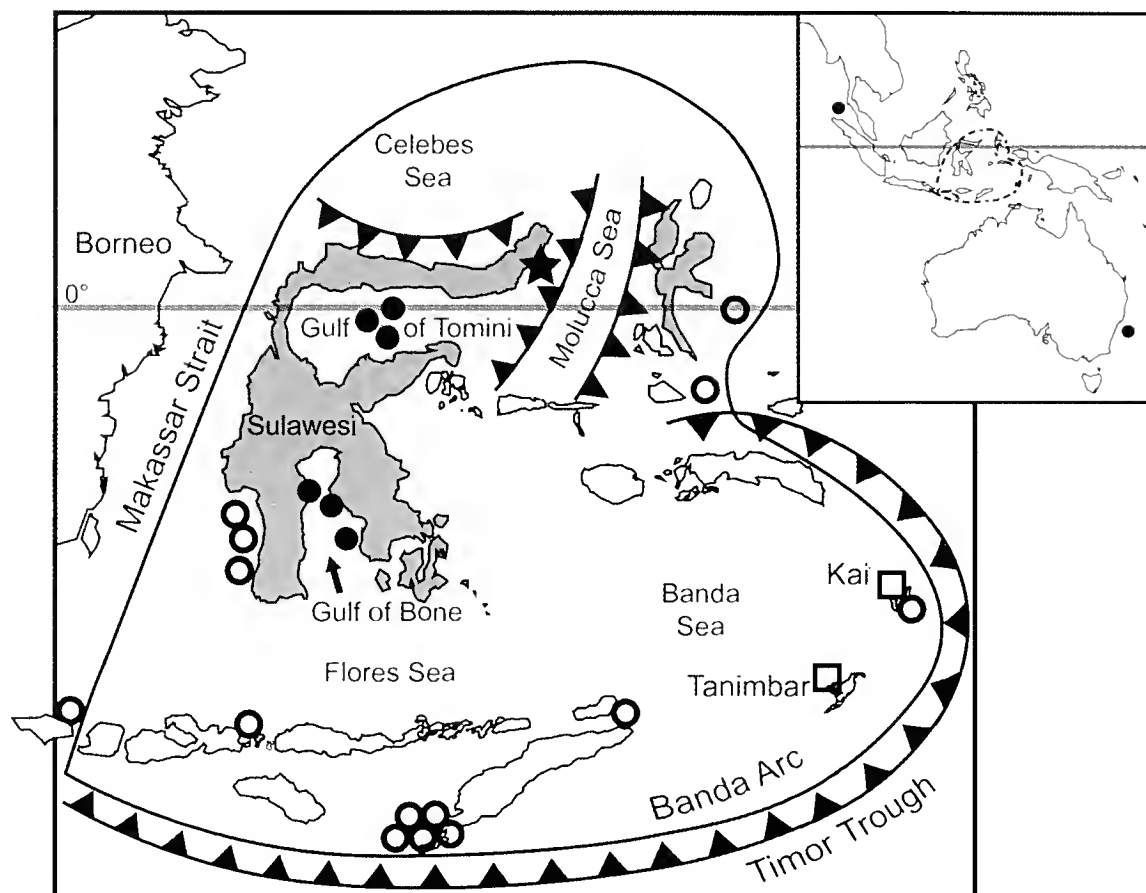
Figure 41. Simplified map of the deep Wallacean region of the Indonesian Archipelago with localities for the new calliotropid species (solid circles) and previously described calliotropids from the Siboga Expedition (open circles) and French KARUBAR Expedition (open squares). The locality of the previously described new gazid genus and species is shown by a solid star. Isolated occurrences in deep-deep-sea basins, gulfs and straits are depicted in the context of primary zones of collision and subduction (solid lines with triangular tick marks) and associated volcanic arcs at plate boundaries where subduction has occurred or is occurring.

2004; Jablonski et al., 2007; Camplin and Hall, 2014) as well as sediment systems with diffusive methane emission and a deep biosphere of chemosymbiotic microbial communities (Schippers et al., 2010; Siegert et al., 2011).

RELATIONSHIP OF SHALLOW AND DEEP BIOGEOGRAPHIC PATTERNS

The patterns and explanations of deep-water biodiversity and connectivity in Indonesia are highly unlikely to correspond with those that have begun to emerge for shallow water taxa. In shallow-water taxa there is a striking disconnect between surface currents and routes of gene flow (e.g., Benzie, 1998, 1999; Benzie and Williams, 1995, 1997; DeBoer et al, 2008), perhaps related to underestimation of the importance of seasonal cycles in the upper-ocean mixed layer in which monsoonal forcing generates reversals in flow directions (Lindstrom et al., 1987; McCreary et al., 2001). Current directions and flow speeds are notably different in deep water. Sills between deep basins impede flow, and the vetigastropod taxa under consideration here lack the feeding planktonic larvae that enhance the dispersal potential of many shallow-water taxa. Deep-water diversity is likewise

unaffected by the diversity increase in reef-associated habitats and the Oligo-Miocene pulse of shallow-water diversification of reef-associated taxa in the Indo-West Pacific (Williams and Duda, 2008).

In fact, it is argued here that modern marine biogeographic patterns in the Indonesian region cannot be understood apart from geologic history. Reconstruction of the entire Cenozoic history of plate boundaries (Hall, 2001, 2002), especially the dramatic effects of episodic volcanic arc processes on marine topography (Hall and Smyth, 2008), argue against simplistic inferences of marine connectivity and historical biogeography based solely on present configurations.

EXPLAINING DISJUNCT DEEP-WATER TAXA IN WALLACEA AND SOUTHERN AFRICA

The disjunct distribution of calliotropid species in deep Pacific waters of Wallacean Indonesia and the far western Indian Ocean has been recognized for more than 100 Years. Schepman (1908) reported *Calliotropis metallica* (Wood-Mason and Alcock, 1891) from four stations in Indonesia. The species is better known from Madagascar and southern Africa, and was described

originally from the Gulf of Mannar in the Indian Ocean. *Calliotropis buccina* Vilvens, 2006, described from Reunion Island in the southwestern Indian Ocean is now reported from the Kai archipelago in southeastern Indonesia as well as the Solomon Islands, adding a third disjunct element (Vilvens, 2007). This peculiar pattern is not restricted to calliotropid gastropods, although it does appear to occur in lineages with a long, pre-Cenozoic geologic history. It is consistent with the hypothesis that these are relictual occurrences of taxa and lineages with ranges that have been fragmented and reduced. Two additional examples are given here.

ABYSSOCHRYSID GASTROPODS

The first is in the distribution of living species of the caenogastropod family Abyssochrysidae Tomlin, 1927. In a revision of the genus, Houbrick (1979) provided a detailed analysis of the shell morphology, anatomy, and radulae of the two living species: one described by Tomlin (1927) from 1645–1828 m off the Cape of Good Hope and the other described by Schepman (1909) from the Sulu Sea in Indonesia. Based on further examination of hydrographic data and search of the fossil record, Houbrick (1979) proposed that these two living abyssochrisids are deep-water relicts of the Paleozoic-Mesozoic superfamily Loxonematoidea (Koken, 1889). Although Houbrick (p. 1) considered his proposal to be "radical", description of new material from deep-sea expeditions (Bouchet, 1991) recognized five species, including a new species from the Makassar Strait in Indonesia and a distribution that is localized in the deep-water settings around Sulawesi.

The Indonesian material examined by Houbrick (1979) included specimens from the ALBATROSS expedition, and it is interesting to note that one of the specimens appears to be from the same locality in the Gulf of Bone as the type of the *Calliotropis* species described above as *C. lamuluensis*. Houbrick did not give the station number or coordinates, but the reported depth is the same as well as the location off Lamulu Point.

Description of a putative abyssochrysid from the middle Eocene of the northwestern Olympic Peninsula in western Washington (Goedert and Kaler, 1996; Kiel, 2008) adds a new paleoenvironmental dimension to the post-Mesozoic disjunct geographic distribution. The Eocene species is known from >50 specimens in a localized methane-derived authigenic carbonate deposit in association with chemosymbiotyic solemyid, lucinid, thyasirid, and vesicomyid bivalves as well as abundant serpulid and vestimentiferan worm tubes.

LIVING COELACANTHS

The same pattern of disjunction is not confined to marine invertebrates. It has received considerable attention with discovery of a second population of the "living fossil" coelacanth genus *Latimeria* off Manado, Sulawesi, Indonesia (Erdmann et al., 1998). The Sulawesi population is separated by a distance of >10,000 km from the African population in the Comros Islands (see Springer, 1999; Holder et al., 1999). Although the two populations must share a common ancestor, there is no available evidence to test alternative historical biogeographic hypotheses.

CONCLUSIONS

Knowledge of the internal phylogenetic structure of Calliotropidae is highly unsatisfactory, although the anatomical, and molecular data are consistent with placement of Calliotropidae in Seguenzioidea. For most of the living species and available genus-group names there are no anatomical or molecular data and no consistent terminology for shell features. There are no published accounts of the behavior of live animals and little information on habitats aside from records of some large-shelled deposit-feeding species with enlarged hindguts in hydrocarbon seep biotopes where primary productivity is greatly enhanced by microbial chemosynthesis. Problems are compounded by the long fossil record and history of paleontological treatments using separate names and classification.

On the positive side, resurgence of interest in deep-sea exploration and use of new sampling methods are adding considerably to the amount of new material available for study. In addition, there seems to be increased interest in describing older material that has been languishing in museum collections. New techniques enable illustration of microsculpture and features that have not been noted previously. This paper draws special attention to the potential of new characters for diagnosing taxa.

The discovery of elevated deep-water diversity of calliotropid gastropods in the Indo-West Pacific, especially in the deep basins in the Wallacean region of Indonesia, should not be surprising in view of new data on regional tectonic history: collision of the Australian, Eurasian, and Philippine Sea plates; development of volcanic island arcs; arc-arc and arc-continent collisions; subduction; deformation, faulting, rotations and translations; openings and closings of distinct deep-water basins, gulfs and straits; and the movement and accretion of microplates. Evolutionary persistence of Indian Ocean faunal elements in Wallacea is not a difficult fate to imagine for taxa arriving on Indian Ocean lithosphere trapped and ultimately subducted in the collision zone.

New understanding of seafloor topography and hydrography of the Indo-West Pacific is in turn related to the shallow and deep-water current systems that affect biogeographic patterns. History and physical oceanography of Indonesian Throughflow and the gateway connection between the Pacific and Indian Oceans is potentially a strong key to understanding some of the puzzling biogeographic connections between southern Africa and Indonesia.

ACKNOWLEDGMENTS

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Latest Oligocene and Miocene whelks (Gastropoda: Neogastropoda: Buccinidae) from Peru

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ABSTRACT

Misifulgur new genus includes fusiform buccinid gastropods with shells that are notably thin medially between the shoulder and base, have moderately long siphonal canals, spiral cords that are well developed anteriorly but often fade posteriorly, an inner lip without plications, a smooth inner surface of the outer lip, and no axial sculpture other than growth lines. The oldest *Misifulgur*, *M. dockeryi* new species, comes from lower Oligocene deposits in Mississippi. While no later records of *Misifulgur* are known from Gulf Coast states or Central America, *Misifulgur* whelks (i.e., *M. sula* (Olsson, 1931), *M. cruziana* (Olsson, 1932), *M. macneili* new species) are the most commonly preserved neogastropods from the latest Oligocene through middle Miocene on sandy substrates at shelf depths in the Peruvian Faunal Province. The most recent *Misifulgur*, *M. montemarensis* new species, lived on protected sandy substrates along the coast of southern Peru during the late Miocene. The late Miocene extinction of *Misifulgur* was contemporaneous with the appearance on the inner shelf of possible competitors, especially muricids of the genus *Chorus* Gray, 1847.

Additional Keywords: Miocene, Mississippi, taxonomy, paleontology, biogeography

INTRODUCTION

The East Pisco Basin was a locus of marine deposition in south-central Peru from the late Eocene until the early Pliocene (DeVries, 1998). Forearc sedimentary strata, which became emergent during the late Pliocene and Quaternary, record shoreface, shallow subtidal, and shelf paleoenvironments (DeVries and Schrader, 1997). Mollusks are abundantly preserved in nearshore deposits and, to a lesser extent, in the medium-grained, bioturbated, and winnowed sandstones associated with inner-shelf water depths. Among neogastropods, the most prominent on the latest Oligocene and Miocene Peruvian shelf were heretofore unrecognized whelks of the family Buccinidae.

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The first evidence of late Oligocene–Miocene Peruvian whelks consisted of three incomplete specimens from the Talara and Progreso forearc basins of northern Peru. These gastropods were mischaracterized by Olsson as two species of muricids, *Acanthina (Chorus) sula* Olsson, 1931 and *Acanthiza (Chorus) sula cruziana* Olsson, 1932. New fossil whelks from the East Pisco Basin and the more southerly Sacaco Basin, including specimens with intact protoconchs and siphonal canals, show that Peruvian whelks were widely distributed and common in shelf environments throughout the Miocene until they became extinct at about 6 Ma.

The Peruvian whelks are similar to some Paleogene buccinids from the southeastern United States included by MacNeil and Dockery (1984) in the genus *Pseudofulgur* MacNeil, 1984, a taxon comprised of fusiform buccinids from the lower Oligocene Byram Formation of Mississippi. MacNeil's genus has been re-evaluated after examining the Peruvian fossils, type specimens of *Pseudofulgur*, and a new specimen provided by D. Dockery (Office of Geology, Department of Environmental Quality, Mississippi).

GEOLOGY

Onshore outcrops of the Talara Basin in northern Peru extend from the Illescas Mountains (6° S) nearly to the Ecuadorian border (3°45′ S). The Progreso Basin passes from northernmost Peru into southwestern Ecuador (Figure 1). Several thousand meters of marginal marine and deeper water sediments accumulated in these forearc basins throughout the Cenozoic (Zúñiga and Cruzado, 1979; Higley, 2004a, 2004b; Martinez et al., 2005). Oligocene and Miocene deposits are especially well developed north of Cabo Blanco (Palacios, 1994). Whelks collected by Olsson (1931) from shallow-water shales at Caleta Mero (3°50′ S) were attributed to the basal upper Oligocene or lower Miocene Heath Formation (Olsson, 1931; Engelhardt and Wood, 1993; Higley, 2004a), an assignment consistent with both current geological mapping (Palacios, 1994) and the concurrent presence of *Turritella woodsi* Lisson, 1925 (= *Turritella conquistadorana* Hanna and Israelsky, 1925), which ranges in southern Peru from

the late Eocene to latest Oligocene (DeVries, 2007b). A single whelk specimen from Quebrada de la Cruz, a few kilometers east of Caleta Cruz (3°38′ S), was attributed to basal sandstones of the upper Oligocene to lower Miocene lower Zorritos Formation, which, depending on the precise locality, is stratigraphically correlative with or conformably overlying Heath shales (Olsson, 1932). Olsson's (1932) stratigraphic attribution is consistent with current mapping (Palacios, 1994) and age assignments (Higley, 2004b).

The East Pisco Basin (Figure 1) is filled with many hundreds, rather than many thousands of meters of

Cenozoic marine sedimentary rock (Montoya et al., 1993; Leon et al., 2008). Four major depositional sequences are recognized, each associated with an eponymous formation: the Paracas (upper Eocene), Otuma (uppermost Eocene), Chilcatay (uppermost Oligocene to lower middle Miocene), and Pisco (middle Miocene to Pliocene) (DeVries, 1998). Fossil whelks in southern Peru are found in the Chilcatay and Pisco depositional sequences, ranging from the base of the former (about 25 Ma) to the upper half of the latter (about 6 Ma). The most southerly occurrence of Miocene Peruvian whelks is in the Sacaco Basin (Figure 1), situated about 50 km south of
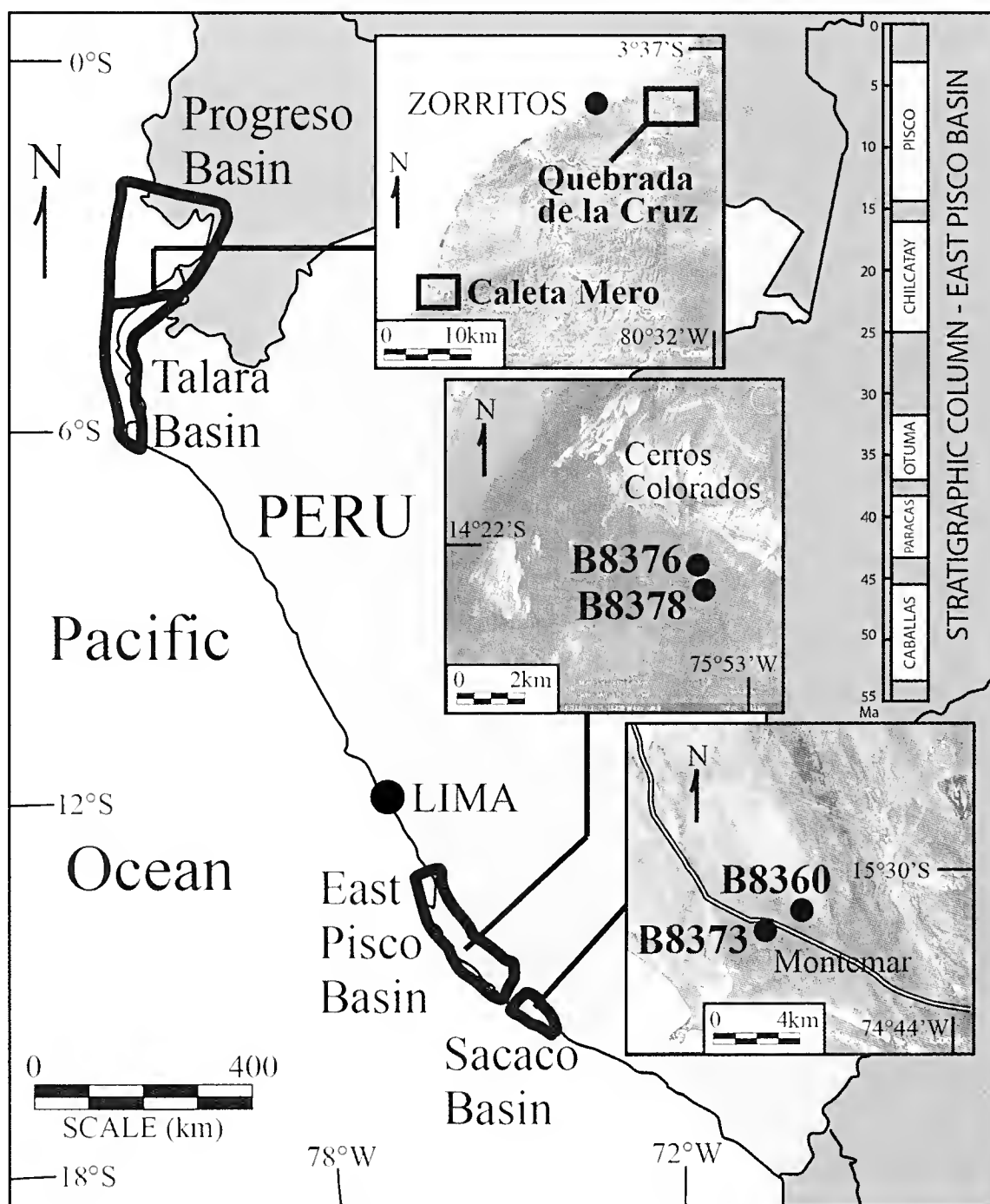
Figure 1. Peruvian Cenozoic forearc basins and type localities of Peruvian species of *Misifulgur*. Progreso and Talara basins after Higley (2004). Upper inset shows type localities of *M. sula* (Olsson, 1931) (Caleto Mero) and *M. cruziana* (Olsson, 1932) (Quebrada de la Cruz). Middle inset shows type locality of *M. macneili* new species (B8376) and a nearby locality (B8378). Lower inset shows type locality of *M. montemarensis* new species (B8360) and a nearby locality (B8373). Inset images are from Google Earth. A stratigraphic column for the Cenozoic section in the East Pisco Basin is shown at upper right.

the East Pisco Basin, where a few hundred meters of inner shelf and nearshore sediments were deposited during the middle to late Miocene and Pliocene (Muizon and DeVries, 1985).

MATERIALS AND METHODS

Specimens from southern Peru were collected by the author. Comparative material was provided by the Academy of Natural Sciences of Philadelphia (Pennsylvania; ANSP), the Office of Geology, Mississippi Department of Environmental Quality (Jackson, Mississippi; MGS), the Paleontological Research Institution (Ithaca, New York; PRI), and the United States National Museum of Natural History (Washington, DC; USNM).

Locality-sample descriptions, listed in the appendix, are designated with a code referencing the author's field notes (DV ××××-××) and a code referencing collections of the University of Washington's Burke Museum of Natural History and Culture (B××××). Lengths (L) and widths (W) are measured in millimeters. Dimensions of broken specimens are enclosed by parentheses. Most figured specimens were coated with ammonium chloride prior to photography. Types and other figured specimens from southern Peru are deposited at the Burke Museum (UWBM) in Seattle and the Laboratorio de Paleontología de Vertebrados, Museo de Historia Natural, Universidad Nacional Mayor de San Marcos (MUSM INV) in Lima, Peru.

SYSTEMATICS

Superfamily Buccinoidea Rafinesque, 1815
Family Buccinidae Rafinesque, 1815

Genus *Misifulgur* new genus

Type Species: *Misifulgur dockeryi* new species. Oligocene, Mississippi.

Diagnosis: Shell fusiform; shell very thin midway between shoulder and base. Protoconch mammillate, paucispiral, smooth, slightly deviated. Axial sculpture of radial orthocline growth lines. Spiral sculpture of primary cords at base, usually becoming weak or obsolete adapically near shoulder. Columellar and parietal calluses absent. Siphonal fasciole obsolete. Inner lip without plications. Inside of outer lip smooth.

Description: Shell medium to large sized, fusiform, very thin medially between shoulder and base. Protoconch mammillate, two to three whorls, smooth, slightly deviated. Spire moderately elevated; sutures variably impressed. Sutural ramp planar, slopes and widths highly variable, marked at shoulder by spiral cord of varying strength. Axial sculpture consisting of radial orthocline growth lines without sutural sinus. Spiral sculpture on smaller whorls with 12 to 20 subequally spaced primary spiral cords;

primary interspaces half as wide to slightly wider than primary cords, U-shaped or flat-bottomed, rarely with a medial secondary spiral cord. Primary spiral cords on later whorls becoming weaker or absent near shoulder and on sutural ramp. Spire whorls with sutural ramp and three to seven primary spiral cords anterior to shoulder. Aperture elongate. Siphonal canal about 20% of shell length, straight to moderately recurved abaxially. Columellar and parietal callus absent; inner lip without plications. Siphonal fasciole obsolete. Inside of outer lip smooth.

Distribution: Early Oligocene, southeastern United States. Late Oligocene to early Miocene, southwestern Ecuador, northern and southern Peru. Middle to late Miocene, southern Peru.

Etymology: 'Misi,' from the native North American Ojibwa word for 'great.'

Remarks: *Misifulgur* new genus includes fusiform Mississippi specimens assigned to *Pseudofulgur* by MacNeil and Dockery (1984) that have flattened spiral cords that fade in prominence posteriorly, a very thin shell medially between shoulder and base, and a smooth inside of the outer lip (Figures 2–5). Excluded are shells that have a lirate and and/or thickened outer lip, a paucispiral mammillate protoconch with closely spaced axial ribs on the last protoconch whorl, and shells with whorls that are not thinned medially, i.e., the holotype of *P. vicksburgensis* (Conrad, 1848) (Figures 6–7), the holotype of *P. lirata* Dockery, 1984, and a new specimen from the Byram Formation of Mississippi referred to *P. lirata* by Dockery (written communication, 2007) (Figures 8, 9), all of which are probably tonnoideans assignable to Ranellidae Gray, 1854 (sensu Beu and Cernohorksy (1986) and Beu (2010)).

Specimens of *Misifulgur* from Mississippi and western South America resemble the ranellids *Linatella caudata* (Gmelin, 1791), a geographically wide-ranging Tethyan cymatiine from the Miocene to the present (Beu, 2010), and *Monoplex weigmanni* (Anton, 1838), a cymatiine with a late Cenozoic Atlantic-Pacific trans-isthmus distribution (Beu, 2010). Shells of both cymatiines, however, are not thinner medially, have a crenulate or lirate inside to the outer lip, exhibit nodulosity at the shoulder that reflects a muted axial sculpture, and on many larger specimens, a callused columella with transverse lirations—all characters absent on specimens of *Misifulgur* of any size.

Modern buccinids and fasciolariids from western South America with a moderately elongate siphonal canal (e.g., *Aeneator fontainei* (d'Orbigny, 1839); *Pleuroploca* spp.; *Solenosteira fusiformis* (Blainville, 1832); see Alamo and Valdivieso (1997) for geographic distribution data) have either axial sculpture, a finely lirate inner margin of the outer lip or lirate structure beneath a smooth inside surface of the outer lip, or both. Species of the muricid genus, *Peonza* Oliveira, 1994, resembles the most strongly keeled examples of *Misifulgur cruziana*, but the nodulosity of the spiral cord on the shoulder, the absence of anterior inflation of the last whorl, and a corresponding

presence of a very narrow and elongate siphonal canal easily distinguish the Eocene-to-Miocene Chilean and Argentinian taxon from *Misifulgur*.

The origin of early Oligocene *Misifulgur* and its systematic position with respect to other buccinids remains obscure. The well-constrained morphological variation of American *Misifulgur* from the early Oligocene to late Miocene makes it unlikely that European Eocene and Miocene taxa cited by MacNeil and Dockery (1984: 140) have a close affinity. Pliocene North Pacific buccinids with posteriorly fading spiral cords cited by those authors, e.g., *Chrysodomus stantoni* Arnold, 1908, may be Californian biogeographic outliers of the northwest Pacific genus, *Clinopegma* Grant and Gale, 1931, which has a stubby recurved siphonal canal with a well developed columellar callus and siphonal fasciole (Figure 10). Northern hemisphere buccinids with longer recurved siphonal canals, i.e., many species of *Neptunea* Linné, 1758, have a sutural platform and a strong spiral cord or keel on the shoulder, as do some large specimens of *M. cruziana*. The pattern of spiral cords for all *Neptunea* species, however, does not vary from the spire whorls to the last whorl, whereas on most large specimens of *Misifulgur*, spiral cords anterior to the shoulder on spire whorls fade to obsolescence on the last whorl.

Pseudofulgur and, by extension, Mississippi specimens herein assigned to *Misifulgur* were compared by Dockery (MacNeil and Dockery, 1984: 140) with the late Miocene *Halia americana* Olsson, 1922, from Panama and Costa Rica (Olsson, 1922; Haas, 1942: 310, unfigured, as "*Halia* cf. *americana*"; Woodring, 1964: 290, as *Ampulla americana* (Olsson, 1922), not *Halia* Risso, 1826; Petuch, 2003: 49). With a deep turrid-like sinus close to the suture (Figures 11, 12), Olsson's Costa Rican specimen cannot be placed in the volutid genus, *Ampulla* Röding, 1798, nor in the buccinid genera, *Pseudofulgur* and *Misifulgur*.

Mansfield (1935) doubted Olsson's (1922) attribution of the "americana" species to the volutid genus, *Halia*, but saw similarities between Olsson's species and the late Miocene Floridian *Neptunea* (?) *alaquaensis* Mansfield, 1935, including the presence of a sutural sinus (Figures 13, 14). Mansfield's species does have spiral sculpture similar to that of *Pseudofulgur* and *Misifulgur*, but its sutural sinus sets it apart from those genera.

Two northern Peruvian buccinid species assigned herein to *Misifulgur*, *M. sula* (Olsson, 1931) and *M. cruziana* (Olsson, 1932), were placed by their author in the muricid taxon, *Acanthina* (*Chorus*), also spelled *Acanthiza* (*Chorus*). Olsson's gastropods are neither *Acanthina* Fischer von Waldheim, 1807 nor *Chorus* Gray, 1847, both ocenebrine muricids with an anterior external groove and associated enrolled labral tooth (DeVries, 1997, 2003). Specimens of *M. sula* and *M. cruziana* have neither. *Acanthina* (*Chorus*) *meroensis* Olsson, 1931, not assigned herein to *Misifulgur*, was also incorrectly assigned to *Acanthina*; specimens do have an anterior external groove (indeed, two such grooves) and at least one labral tooth, but the square-bottomed groove and spatulate tooth differ from the V-shaped groove and enrolled tooth of *Acanthina*

and *Chorus*. *Acanthiza* (*Chorus*) *solida* (Nelson, 1870) and *Acanthiza* (*Chorus*) *voluta* Olsson, 1932, both Peruvian taxa, are neither *Misifulgur*, *Acanthina*, nor *Chorus*. Olsson's "voluta" species has been referred to the pseudolivid genus, *Testallium* Vermeij and DeVries, 1997 (Vermeij, 1998).

Misifulgur dockeryi new species
(Figures 2–5)

Pseudofulgur vicksburgensis (Conrad, 1848).—MacNeil and Dockery, 1984: 141, pl. 32, fig. 5; pl. 52, fig. 13; not pl. 32, fig. 11.

Diagnosis: Shell length to 45 mm. Sutural ramp weakly planar, sloping anteriorly 45 degrees. Spiral sculpture of about 20 broad primary spiral cords between base and shoulder. Secondary spiral threads present on both sides of shoulder inflection.

Description: Shell length to 45 mm, fusiform, moderately constricted, inflection two-thirds distance from last-whorl suture to anterior end; very thin medially between shoulder and base. Protoconch unknown. Teleoconch with five to six whorls. Spire moderately elevated; sutures strongly impressed. Sutural ramp weakly planar, sloping anteriorly about 45 degrees from suture, with a weak primary spiral cord at shoulder inflection. Axial sculpture of radial orthocline growth lines, twisted adaperturally at suture. Spiral sculpture of about 20 broad flat-topped primary spiral cords between base and shoulder, subequally spaced, becoming obsolete adapically towards shoulder, replaced in part by closely spaced secondary spiral cords and threads on both sides of shoulder. Primary interspaces half as wide to as wide as primary spiral cords, flat-bottomed, rarely with an intercalated secondary spiral cord or tertiary thread. Spire whorls with sutural ramp, shoulder and four or five prominent primary spiral cords. Aperture elongate, ovate. Siphonal canal 20 percent of shell length, nearly parallel to shell axis, broadly open. Columellar and parietal callus absent. Siphonal fasciole obsolete. Inner lip without plications. Inside of outer lip smooth.

Type Material: MGS 1227, holotype, locality 115, L 22.9, W (15.0). Byram Formation, lower Oligocene.

Type Locality: MGS locality 115, east side Highway 61 across from the Anderson Tully Lumber Company at the boundary of Sections 12 and 35, T.16 N., R.3 E. (MacNeil and Dockery, 1984: 405).

Other Material Examined: USNM 136798, USNM locality 259 (top of bluff, Vicksburg, Warren County, Mississippi), H 42.2, W 21.9. Byram Formation (Marl Member), lower Oligocene.

Distribution: Lower Oligocene, Byram Formation, Mississippi.
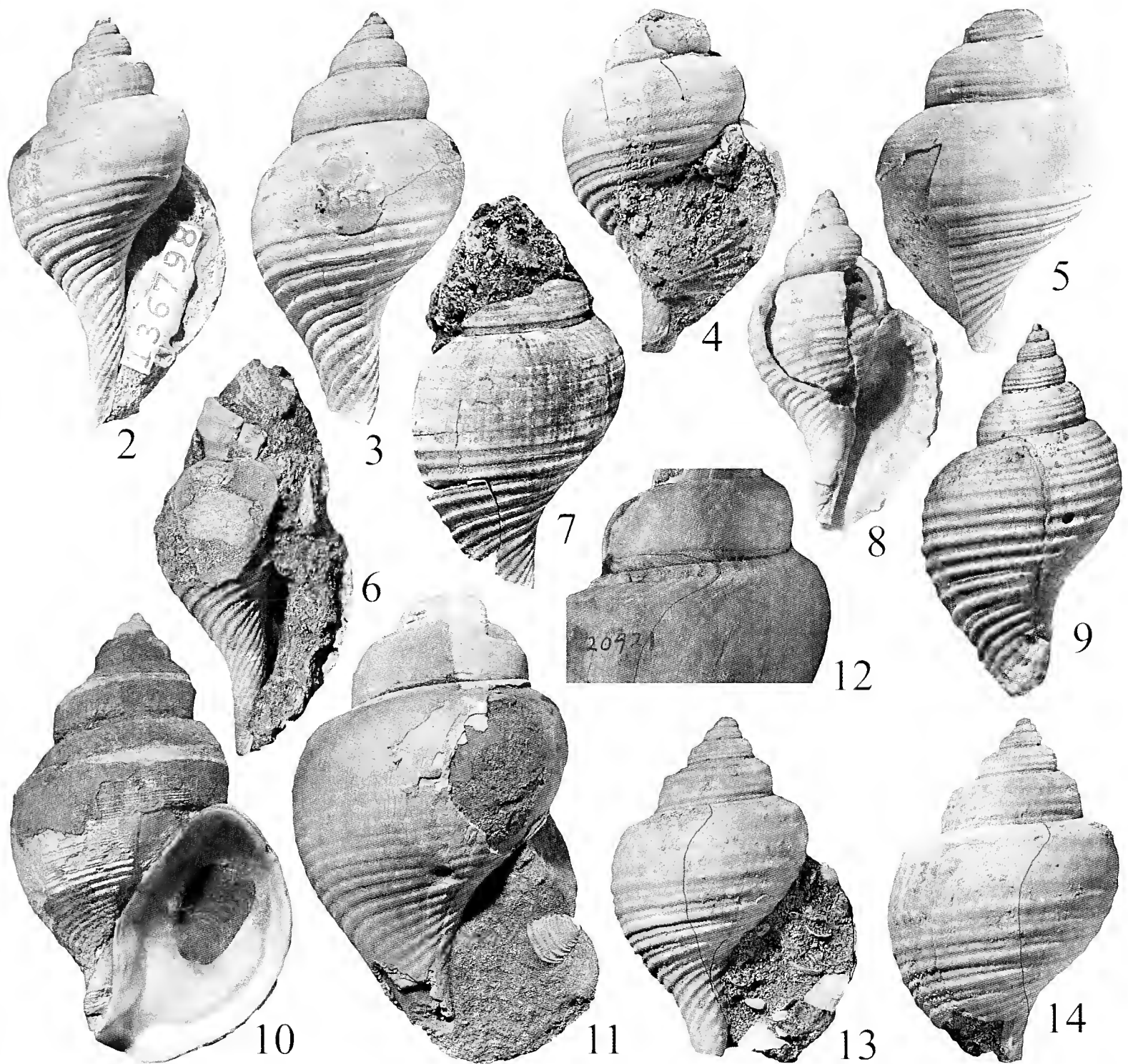
Figures 2–14. Gastropods assigned to or compared with *Pseudofulgur* MacNeil, 1984 by MacNeil and Dockery (1984). **2–5.** *Misifulgur dockeryi* new genus new species. Mississippi. Early Oligocene. **2.** USNM 136798. USGS locality 259. Apertural view. Length 42.2 mm. **3.** USNM 136798. Abapertural view. **4.** MGS 1227. MGS locality 115. Holotype, apertural view. Length 22.9 mm. **5.** MGS 1227. Abapertural view. **6–9.** *Pseudofulgur vicksburgensis* (Conrad, 1848). Mississippi. Early Oligocene. **6.** ANSP 13475. Holotype. Apertural view. Length of exposed shell is 21.4 mm. **7.** ANSP 13475. Abapertural view. **8.** MGS 1905. Apertural view. Length 22.4 mm. **9.** MGS 1905. Abapertural view. **10.** *Clinopegma magnum* (Dall, 1895). UWBM 98677. Bering Sea. Recent. Apertural view. Length 71.2 mm. **11, 12.** *Halia americana* Olsson, 1922. PRI 20921. Holotype. Near Mt. Hope, Panama. Late Miocene. **11.** Apertural view. Length 65.4 mm. **12.** Lateral close-up showing sutural sinus, including portion lapping onto penultimate whorl. **13, 14.** *Neptunea* (?) [sic] *alaquaensis* Mansfield, 1935. USNM 373139. Holotype. Station 12046, Vaughan Creek, upper locality, Walton County, Florida. Late Miocene. **13.** Apertural view showing sutural sinus. Length 35 mm. **14.** Abapertural view showing sutural sinus.

Etymology: Named in honor of David T. Dockery, III (Mississippi Office of Geology), in recognition of his work on fossil Cenozoic mollusks of the southeastern United States.

Remarks: Specimens of *Misifulgur dockeryi* new species differ from those of *Pseudofulgur vicksburgensis* in having a thin shell medially between shoulder and base and a smooth inner surface of the outer lip. Specimens of

the latter species have a strongly lirate inner surface of the outer lip and no mid-whorl thinning. Specimens of *M. dockeryi* lack axial sculpture, whereas those of *P. vicksburgensis* have growth lines thickened to the point of becoming low, flat, axial ribs (Figures 7, 9).

Populations of *Misifulgur dockeryi*, as well as *Pseudofulgur* spp., inhabited sandy and muddy substrates on an aggrading continental shelf (Coleman, 1983).

Misifulgur sula (Olsson, 1931)
(Figures 15–18)

Acanthina (Chorus) sula Olsson, 1931: 107, pl. 18, figs 1, 2.

Diagnosis: Shell fusiform, strongly constricted towards base. Sutural ramp planar to slightly concave, steeply sloping anteriorly from suture. Spire whorls with three or four well-developed spiral cords anterior to shoulder.

Description: Estimated shell length to 50 mm; fusiform, strongly constricted, inflection two-thirds distance from last-whorl suture to anterior end. Shell very thin medially between shoulder and base. Protoconch unknown. Teleoconch with at least three whorls. Spire moderately elongate, sutures moderately impressed. Sutural ramp planar, sloping anteriorly 45 degrees from suture, with low flattened primary spiral cord at shoulder. Axial sculpture of radial orthocline growth lines, bent adaperturally at suture. Spiral sculpture of about 17 primary spiral cords between base and shoulder, posteriormost three cords flattened and weak to obsolete. Sutural ramp smooth. Interspaces flat-bottomed, wider than spiral cords at mid-whorl, lacking intercalated secondary spiral cords. Spire whorls with smooth sutural ramp, prominent shoulder, and three or four strong primary spiral cords anterior to shoulder. Aperture elongate, ovate. Siphonal canal estimated at 20 percent of shell length, narrow, straight or recurved abaxially. Columellar and parietal callus absent. Siphonal fasciole obsolete or weakly developed. Inner lip without plications. Inside of outer lip smooth.

Type Material: PRI 2104, holotype, L (43.3), W 29.0; PRI 2105, paratype, L (27.4), W 18.0.

Type Locality: Caleto Mero, northern Peru (Figure 1, upper inset), early Miocene.

Distribution: Uppermost Oligocene to lower Miocene, Heath and lower Zorritos formations, northern Peru. Lower Miocene, Posorja, Ecuador (Olsson, 1931).

Remarks: Specimens of *Misifulgur sula* are more sharply constricted anteriorly than those of the Gulf coast *M. dockeryi* and the latest Oligocene to early Miocene Peruvian *M. macneili* new species, have a wider sutural platform and more prominent corded shoulder, and have spire whorls with three or four well-developed spiral cords anterior to the shoulder, rather than the four or five of *M. dockeryi* and six or seven of *M. macneili*. The sutural platform is more steeply sloped anteriorly

than most specimens of *M. cruziana*, creating a more fusiform and less turreted profile.

The holotype (PRI 2104) of *Misifulgur sula* has a siphonal canal that is moderately recurved, unlike the paratype (PRI 2105) and specimens assigned to other species of *Misifulgur*, and growth lines on the last whorl of the holotype trace a small sutural sinus that is absent for other species of *Misifulgur*. New material from northern Peru might indicate the need for a taxonomic revision of *M. sula*.

Misifulgur macneili new species
(Figures 19, 20)

Diagnosis: Shell fusiform, moderately constricted towards base. Sutural ramp narrow, planar, steeply sloping anteriorly. Primary spiral cords well developed between base and shoulder. Spire whorls with six or seven spiral cords.

Description: Estimated shell length to 70 mm, fusiform, moderately constricted, inflection two-thirds distance from last-whorl suture to anterior end. Shell thin medially between shoulder and base. Protoconch unknown. Teleoconch with at least five whorls. Spire moderately elongate, sutures moderately impressed. Sutural ramp narrow, sloping anteriorly 60 degrees from suture, with low flattened spiral cord at poorly defined shoulder. Axial sculpture of radial orthocline growth lines, bent adaperturally at suture. Spiral sculpture of about 18 primary spiral cords between base and shoulder, with anterior cords stronger and separated by equally wide interspaces; posterior cords weaker, flattened, and with interspaces half as wide as cords. Some anterior interspaces with an intercalated secondary spiral cord. Spire whorls with smooth, steeply sloping sutural ramp, rounded and poorly defined shoulder, and seven equally strong spiral cords anterior to shoulder. Aperture oval. Siphonal canal estimated at 20 percent of shell length, weakly recurved abaxially. Columellar callus absent; parietal callus not visible. Siphonal fasciole obsolete. Inside of outer lip smooth.

Type Material: UWBM 98670, holotype, B8376 (type locality), L (44.8), W 27.6; UWBM 104229, paratype, B8376, L (30.8); UWBM 104230, paratype, B8378, L (47.2), W 32.0.

Type Locality: B8376, southwest of Cerros Colorados, East Pisco Basin (Figure 1, middle inset), south-central Peru.

Other Material Examined: UWBM 98671, B8358, L (47.6), W (42.4); MUSM INV 200, B8358, L (49.2), W (39.9); B8378, two fragments.

Distribution: Chattian to Burdigalian, Chilcatay depositional sequence, East Pisco Basin, south-central Peru.

Etymology: Named in memory of F. Stearns MacNeil, posthumously a co-author with David T. Dockery of a 1984 study of Oligocene mollusks from Mississippi and author of the genus, *Pseudofulgur*.
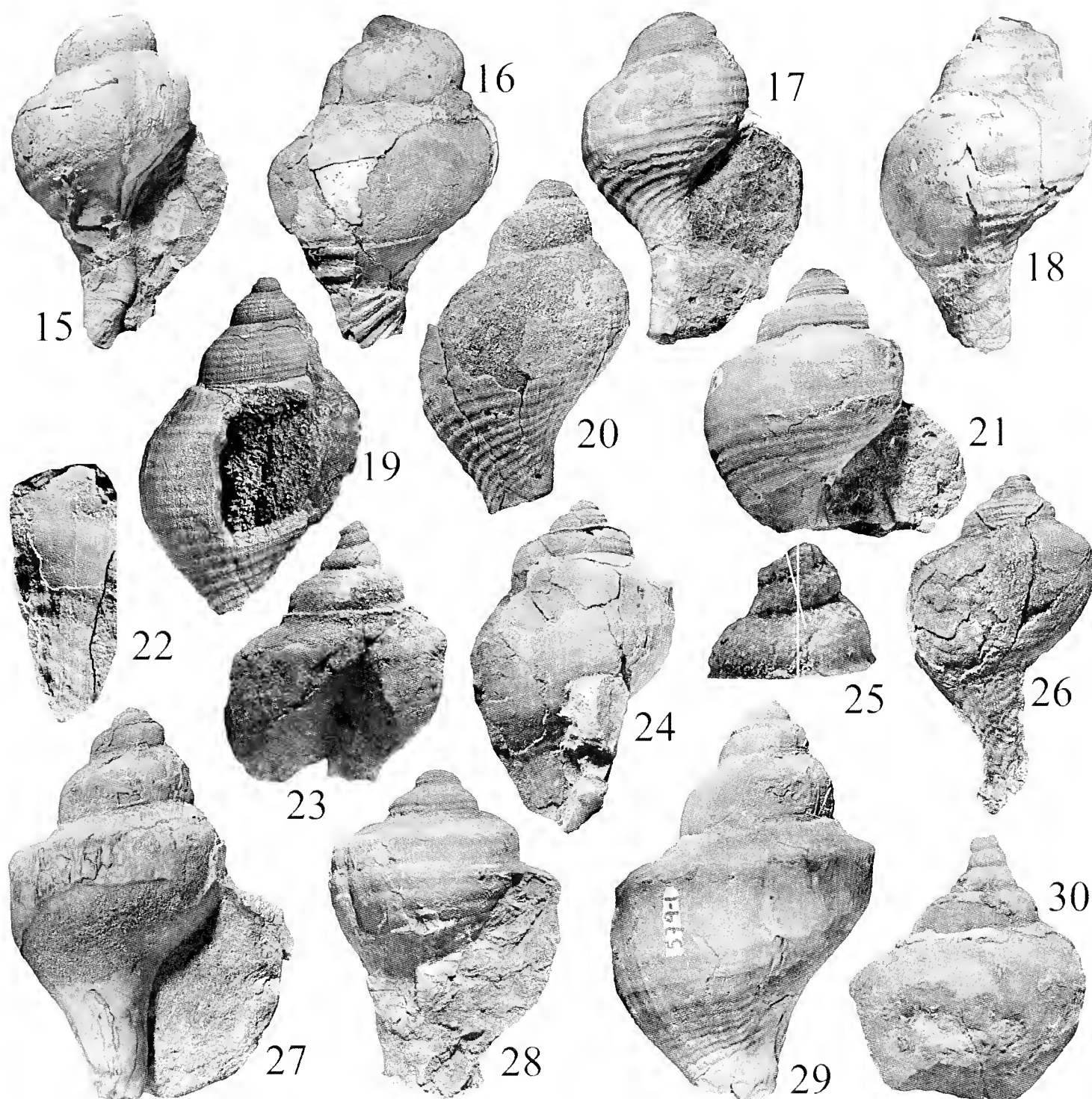
Figures 15–30. *Misifulgur species.* **15–18.** *Misifulgur sula* (Olsson, 1931). Caleto Mero, Talara Basin, northern Peru . Early Miocene.
15. PRI 2104. Holotype. Apertural view. Partially decorticated, partially an internal mold. Length 43.3 mm. **16.** PRI 2104. Abapertural
view. **17.** PRI 2105. Paratype. Apertural view. Length 27.4 mm. **18.** PRI 2105. Abapertural view. Partially decorticated. **19, 20.** *Misifulgur
macneili* new species. East Pisco Basin, south-central Peru. Early Miocene. **19.** UWBM 104230. B8378. Paratype. Abapertural view.
Siphonal canal and portion of last whorl missing. Length 47.2 mm. **20.** UWBM 98670. B8376. Holotype. Abapertural view. Portion of
siphonal canal missing. Partially an internal mold. Length 44.8 mm. **21–30.** *Misifulgur cruziana* (Olsson, 1932). **21.** PRI 2307.
Holotype. Quebrada de la Cruz, Progreso Basin, northern Peru. Early Miocene. Apertural view. Anterior is missing. Length 28.2 mm.
22. UWBM 98656. B8316, East Pisco Basin, south-central Peru. Middle Miocene. Outer lip: fragment of smooth inside of posterior
portion (upper half) and mold of spirally corded exterior of anterior portion (lower half). Leading edge of outer lip at right. Length of
fragment + mold is 28.7 mm. **23.** UWBM 98652. B8316. Abapertural view. Anterior end missing, largest visible whorl partially
decomposed/dissolved. Length 23.7 mm. **24.** UWBM 98656. Abapertural view. Length 55.2 mm. **25.** UWBM 98652. Close-up of
mammillate deviated protoconch. **26.** UWBM 98656. Lateral view. Partially an internal mold at center left of image. **27.** UWBM 98666.
B8371, East Pisco Basin, south-central Peru. Middle Miocene. Apertural view. Portion of siphonal canal missing, partially abraded by
wind-blown sand. Length 64.5 mm. **28.** MUSM INV 194. B8313, East Pisco Basin, south-central Peru. Middle Miocene. Apertural view
of partly erushed specimen. Length 48.2 mm. **29.** UWBM 98666. Lateral view. Partially an internal mold at left on spire. **30.** UWBM
98654. B8316. Abapertural view showing mammillate deviated protoconch. Anterior end missing. Anteriormost whorls decorticated or
with exposed internal mold. Length 19.3 mm.

Remarks: Specimens of *Misifulgur macneili* new species are less constricted towards the base and have a narrower sutural ramp than those of *M. sula*, which otherwise is the species of *Misifulgur* that *M. macneili* most resembles. The anterior and mid-whorl spiral cords on both *M. macneili* and *M. sula* are less flattened, narrower, and with wider interspaces than on specimens of *M. cruziana* and *M. montemarensis* (see below).

At most localities, specimens of *Misifulgur macneili* and *M. cruziana* occur together. The latter species is highly variable in terms of spire height, width and slope of the sutural platform, and the onset of spiral cord obsolescence on later whorls. *Misifulgur macneili* is not thought to be a variant of *M. cruziana* for the following reasons. First, specimens of *M. macneili* have six or seven spiral cords anterior to the shoulder on spire whorls; all variants of *M. cruziana* have three or four. Second, the posterior spiral cords on specimens of *M. macneili* flatten but do not fade to obsolescence on later whorls. On all variants of *M. cruziana*, some posterior spiral cords do disappear. Lastly, the shoulder on specimens of *M. macneili* is barely angled, whereas shoulders on the least tabulate variants of *M. cruziana* have a distinct angulation at the shoulder that coincides with a strong spiral cord.

Misifulgur macneili occurs at two closely situated sites near the base of the Chilcatay depositional sequence in coarse-grained sandstone and fine gravel (Figure 1, middle inset). Specimens are part of a diverse molluscan assemblage that includes gastropods overgrown with bryozoans or small colonies of barnacles. The *Misifulgur*-bearing horizon is correlative with nearby oyster banks that lap against outcrops of crystalline paleo-basement. A latest Oligocene age is inferred from the stratigraphic position of the *Misifulgur* specimens close to the transgressive base of the Chilcatay depositional sequence (DeVries, 1998). The youngest specimens were collected from within the mid-section of the type section of the Chilcatay Formation. Their age is inferred to be about 18 Ma, based on diatoms in overlying tuffaceous and diatomaceous sandstone (DeVries, 1998).

Misifulgur cruziana (Olsson, 1932)
(Figures 21–37)

Acanthiza (*Chorus*) *sula cruziana* Olsson, 1932: 185, pl. 20, fig. 7.
(?) *Chorus cruzianus* (Olsson).—Marks, 1951: 23, 30, also unpaginated figs 5, 7.
(?) *Fasciolaria*? [sic] sp. Marks, 1951: 28, also unpaginated fig. 7.

Diagnosis: Shell length to 120 mm. Sutural ramp planar, sloping anteriorly five to 45 degrees from suture. Primary spiral cord on shoulder strong or keeled on large specimens.

Description: Estimated shell length to 120 mm, fusiform in small specimens, moderately to strongly constricted with inflection about 60 percent of distance from last-whorl suture to anterior end; later whorls posteriorly inflated, deeply constricted, and strongly tabulate in some larger specimens. Shell very thin medially between shoulder and base. Protoconch mammillate, smooth, at least two whorls, slightly deviated. Teleoconch with five whorls. Spire moderately elongate, sutures moderately impressed. Sutural ramp planar, sloping anteriorly 45 degrees from suture on small and medium-sized specimens; on large specimens, sutural ramp planar to concave, sloping anteriorly five to 45 degrees from suture. Shoulder angulate, defined by rounded primary spiral cord, keeled on some large specimens. Axial sculpture of orthocline radial growth lines, often bent adaperturally at suture. Earliest spire whorls with smooth sutural ramp and three or four primary spiral cords anterior to shoulder. Last whorl on small specimens with about 17 broad primary spiral cords between base and shoulder, with posteriormost three diminished, flattened, and more widely spaced. Primary interspaces U-shaped to flat-bottomed, becoming as wide as primary cords adapically towards shoulder, rarely with an intercalated secondary spiral cord. Either side of shoulder sometimes with closely spaced subdued secondary spiral cords; sutural ramp with primary spiral cords absent or with one spiral cord situated medially or close to suture. Larger specimens with broad smooth concavity bounded by shoulder and primary spiral cord near midpoint of whorl. Anterior half of last whorl on large specimens with about 12 spiral cords, spaced more closely towards base. Aperture ovate and elongate in small specimens, quadrate in large specimens. Siphonal canal about 20 percent of shell length, recurved abaxially, broadly open. Columellar or parietal callus absent. Inner lip without plications. Siphonal fasciole obsolete. Inside of outer lip smooth.

Type Material: PRI 2307, holotype, L (28.2), W 26.1.

Type Locality: Quebrada de La Cruz, northern Peru (Figure 1, upper inset), early Miocene.

Other Material Examined: MUSM INV 190, B8316, middle Miocene, L (29.7), W (28.8); MUSM INV 191, B8316, L (29.2), W 17.7; MUSM INV 192, B8316, L (28.9), W 28.4; MUSM INV 193, B8316, L 62.0, W (47.1); MUSM INV 194, B8313, middle Miocene, L (48.2), W 34.1; MUSM INV 195, B8305, early Miocene, L (28.2), W (26.1); MUSM INV 196, B8371, middle Miocene, L (54.4), W 40.0; MUSM INV 197, B8371, L (43.5), W 31.3; MUSM INV 198, B8371, L (50.1), W (53.4); MUSM INV 199, B8358, early Miocene, L (39.5); UWBM 98652, B8316, L (23.7), W 19.0; UWBM 98653, B8316, L (29.4), W 28.0; UWBM 98654, B8316, L (19.3), W 16.6; UWBM 98655, B8316, L 30.9, W (19.9); UWBM 98656, B8316, L (53.0), W 33.6; UWBM 98657, B8316, L (57.3), W 47.3; UWBM 98658, B8364, middle Miocene, L (47.0), W 34.7; UWBM 98659, B8362, middle Miocene, L (48.0), W (31.2); UWBM 98660, B8362, L (28.2), W (25.5); UWBM 98661, B8372, middle Miocene, L (37.8), W (46.5); UWBM 98662, B8305, L (65.3), W (52.5); UWBM 98663,
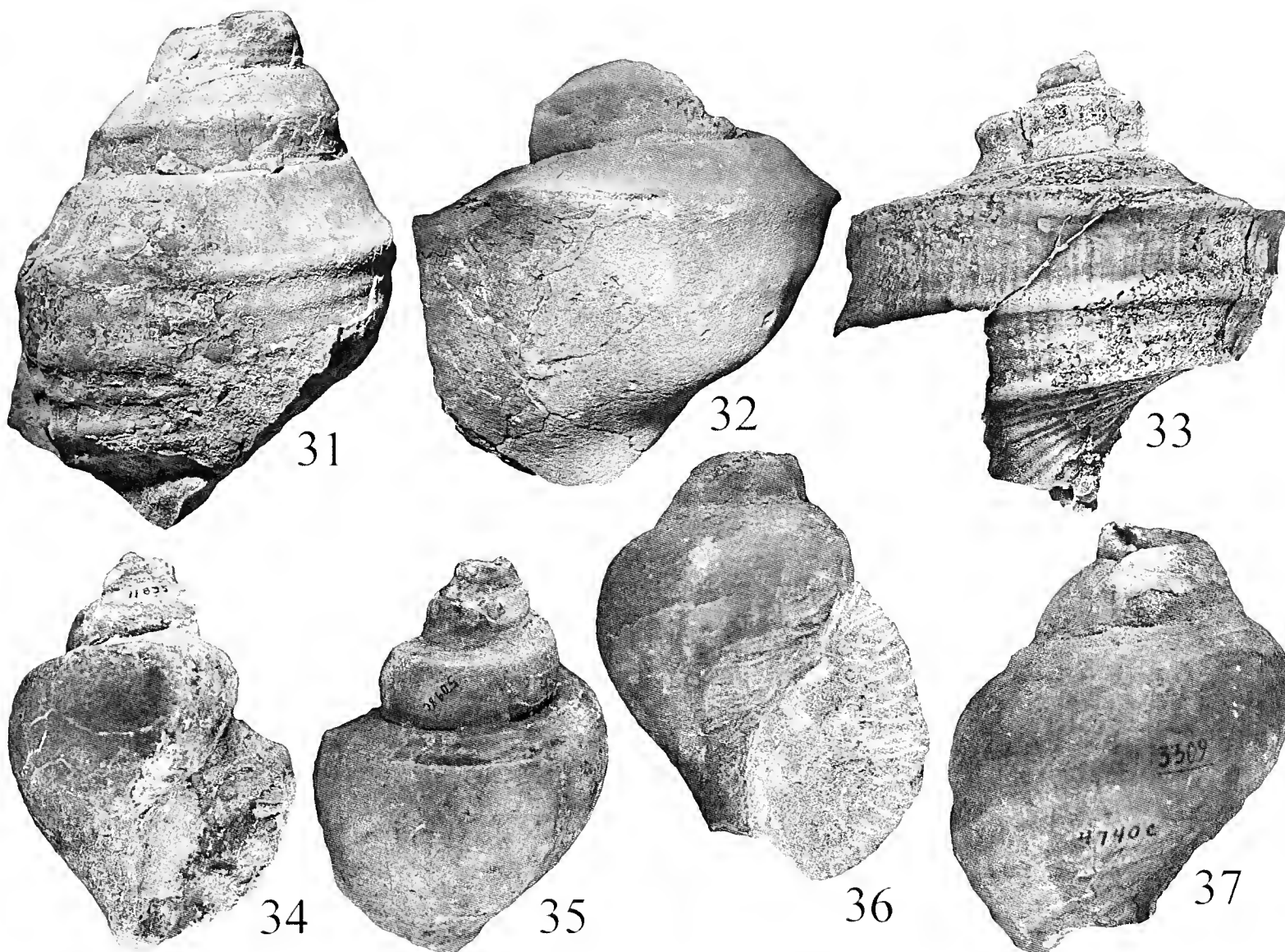
Figures 31–37. *Misifulgur species.* **31–33.** *Misifulgur cruziana* (Olsson, 1932). Large specimens from East Pisco Basin, south-central Peru. Late Oligocene to early Miocene. **31.** UWBM 104232, BS361. Abapertural view. Partially decorticated. Length 83.6 mm. **32.** UWBM 104231, BS361. Abapertural view. Internal mold. Length 63.1 mm. **33.** UWBM 104233, BS358. Abapertural view. Rubber cast of external mold in concretion. Length 61.0 mm. **34–37.** *Misifulgur cruziana* (Olsson, 1932). Molds from the Progreso Basin of southwestern Ecuador (Marks, 1951). **34.** PRI 68827, PRI locality 5098C. Progreso Formation, middle to lower Miocene. Apertural view. Internal mold, most of siphonal canal missing. Image taken without ammonium chloride. Length 107 mm. **35.** PRI 68827. Abapertural view. **36.** PRI 68826, PRI locality 4740C. Upper Tosagua Formation, lower Miocene. Apertural view. Internal mold, anterior end missing. Image taken without ammonium chloride. Length 79 mm. **37.** PRI 68826. Abapertural view.

BS305, L (34.6), W (26.4); UWBM 98664, BS376, early Miocene, L (25.0), W (23.0); UWBM 98665, BS376, L (24.7), W 18.0; UWBM 98666, BS371, L (64.5), W 46.3; UWBM 98667, BS371, L (48.0); UWBM 98668, BS371, L (69.4), W (55.6); UWBM 98669, BS358, L (48.1), W (44.4); UWBM 98676, BS366, late Miocene, L (61.4), W (42.8); UWBM 104231, BS361, early Miocene, L (63.1), W (62.7); UWBM 104232, BS361, L (83.6), W (62.5); UWBM 104233, BS358, L (61.0), W (57.0); UWBM 104234, BS363, late middle Miocene, L (78.9), W 65.3; PRI 68826, L (79), W 64; PRI 68827, L (107), W 78. Also BS359, BS365, BS369, BS370, BS333, BS374, BS375, BS377, BS343, BS379.

Distribution: Aquitanian, Chilcatay depositional sequence, south-central Peru; lower Zorritos/Heath formations, northern Peru. Dos Bocas Member, Tosagua For-

mation, Progreso Basin, southwestern Ecuador. Burdigalian to early Tortonian, Chilcatay and Pisco depositional sequences, south-central Peru. Tosagua and Progreso formations, Progreso Basin, southwestern Ecuador.

Remarks: The incomplete holotype of *Misifulgur cruziana* from northern Peru is identical with more complete medium-sized specimens from the East Pisco Basin. Specimens of *M. cruziana* from south-central Peru include examples with paucispiral, deviate, mammillate protoconchs (Figures 23, 25, 30), a complete siphonal canal (Figure 26), and highly variable specimens much larger than the northern Peruvian holotype (Figures 31–33), in which the last whorls may be broader, more inflated posteriorly, and with keeled shoulders bounded anteriorly and posteriorly by broad, shallow, smooth concavities (Figures 29, 33).

Misifulgur cruziana was the most common medium-sized to large carnivorous gastropod on the Peruvian continental shelf from the early to early late Miocene, living far enough offshore for sardine scales to be embedded in the sandy matrix, i.e., at water depths of 30 meters or greater (DeVries and Pearcy, 1982). The youngest specimen was found near the base of upper Miocene outcrops at Cerro Blanco, in the Río Ica valley near Ocucaje (UWBM 98676), where medium-grained sandstone lies nonconformably upon a rugged basement of crystalline basement rock (locality BS366). An ash bed (DV 494-5Snee) 68 meters above the *Misifulgur*-bearing bed yielded an ^{40}Ar-^{39}Ar date of 6.85 ± 0.07 Ma (L. Snee, United States Geological Survey, written communication, 1987), consistent with a late late Miocene age indicated by diatoms from nearly the same horizon (H. Schrader, University of Bergen, Norway, written communication, 1988) and other ^{40}Ar-^{39}Ar ash dates from correlative same strata (Brand et al., 2011).

A buccinid mold (PRI 68826; figs 36, 37) attributed by Marks (1951) to *Misifulgur cruziana* (cited as *Chorus cruziana*) was collected in southwestern Ecuador, 1.75 kilometers west of Carrizal (estimated locality: 02°06'S, 80°27'30"W, based on comparison of data obtained from MapCarta and Google Earth). A second mold (PRI 68827; figs 34, 35), identified as *Fasciolaria*? sp. [sic] by Marks (1951) but similar to *Misifulgur* molds from Peru and Ecuador, was collected at IPC locality 11895 (P. Plocic, Paleontological Research Institution, written communication, 26 May 2016; additional locality data are unavailable). According to Marks (1951), the Carrizal specimen was collected from cross-bedded sandstones of inner shelf origin from the upper Subibaja Formation, assigned an early Miocene age based on correlations with mollusks in Peru and foraminifera identified by R. M. Stainforth (1948). The Carrizal locality is more recently mapped into the lower Miocene Dos Bocas Member of the Tosagua Formation (Longo and Baldock, 1982). The "*Fasciolaria*" mold (PRI 68827), as well as additional specimens of "*Chorus cruziana*' cited by Marks (1951), were collected from the marine to brackish-water, middle to upper Miocene Progreso Formation (Marks, 1951); its age is supported by more recent authors (Longo and Baldock, 1982). Both Ecuadorian molds have a shape that falls within the broad range shown by Peruvian specimens.
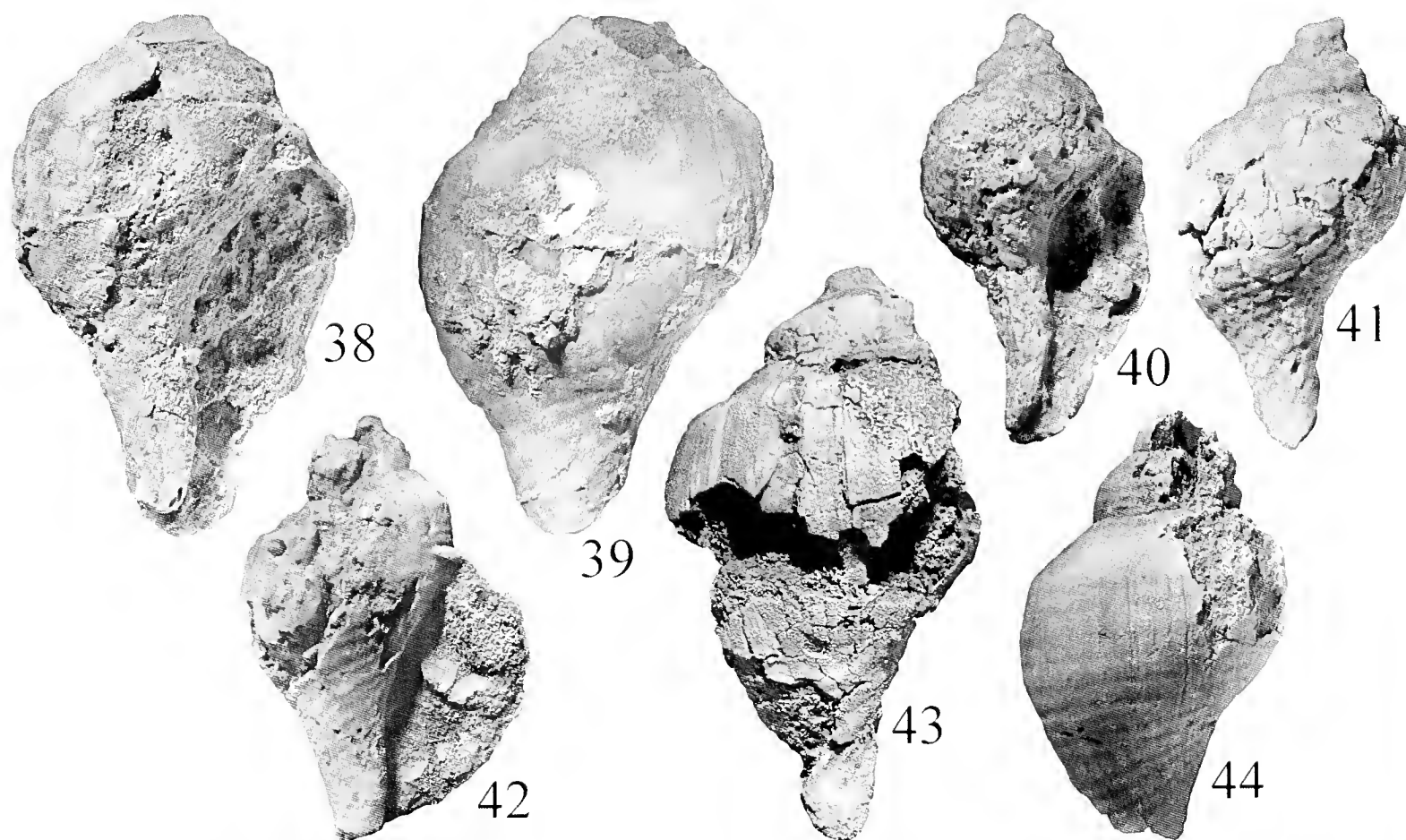
Figures 38–44. *Misifulgur montemarensis* new species. Late Miocene. **38.** UWBM 98672, BS360. Holotype. Sacaco Basin, southern Peru. Apertural view. Shell material partially dissolved, internal mold partially visible. Length 67.9 mm. **39.** UWBM 98672. Abapertural view. Most of spire missing. **40.** UWBM 98674, BS373. Paratype. Sacaco Basin, southern Peru. Apertural view; note mammillate protoconch. Shell material partially dissolved. Length 26.4 mm. **41.** UWBM 98674. Abapertural view. Shell material partially dissolved. **42.** UWBM 98673, BS373. Paratype. Apertural view. Portion of siphonal canal and spire missing, partially an internal mold. **43.** UWBM 98675, BS359. East Pisco Basin, south-central Peru. Abapertural view. Portions of last whorl missing. Length 77.2 mm. **44.** UWBM 98673. Abapertural view.

Misifulgur montemarensis new species
(Figures 38–44)

Diagnosis: Shell length to 110 mm, fusiform, weakly constricted towards base. Sutural ramp weakly planar, sloping anteriorly 50 to 70 degrees from suture. Spiral sculpture of about 16 very broad primary spiral cords between base and shoulder, diminished in strength near shoulder.

Description: Shell to 110 mm long, fusiform, weakly constricted, inflection about 60 percent distance from last-whorl suture to anterior end; shell very thin medially. Protoconch mammillate, smooth, at least two whorls, slightly deviated. Teleoconch of four to five whorls. Spire moderately elevated, sutures weakly impressed. Sutural ramp weakly planar, sloping anteriorly 50 to 70 degrees from suture. Shoulder with small inflection and weak primary spiral cord. Axial sculpture of fine, closely spaced, orthocline, radial growth lines. Spiral sculpture on last whorl of about 16 broad, low, primary spiral cords between base and shoulder, diminishing in strength near shoulder. Primary interspaces broadly U-shaped, narrower than primary spiral cords, without intercalated spiral elements. Spire whorls with sutural ramp and five primary spiral cords, one on sutural ramp and three to four from shoulder anteriorward. Aperture elongate, ovate. Siphonal canal 20 percent of shell length, narrow, open, nearly straight. Columellar and parietal callus absent or nearly so; inner lip without plications. Siphonal fasciole obsolete. Inside of outer lip smooth.

Type Material: (all late Miocene): UWBM 98672, B8360 (type locality), holotype, L (67.9), W 45.4; UWBM 98673, B8373, paratype, L (34.6), W 23.2; UWBM 98674, B8373, paratype, L 26.4, W (13.9).

Type Locality: B8360, eastern flank of Montemar hills, between Lomas and Sacaco, southern Peru. Late Miocene, about 6–8 Ma (Figure 1, lower inset).

Other Material Examined (all late Miocene): MUSM INV 201, B8368, L 102.8, W (49.0); MUSM INV 202, B8367, L (72.9), W (39.7); UWBM 98675, B8359, L (77.2), W (42.2).

Distribution: Late Miocene, southern Peru.

Etymology: Named for the Montemar paleo-island near Lomas, Peru, in the lee of which *Misifulgur*-bearing upper Miocene tuffaceous sands were deposited.

Remarks: Specimens of *Misifulgur montemarensis* have planar and steeply dipping sutural ramps and poorly defined shoulders, even on the largest specimens. Primary spiral cords on specimens of *M. montemarensis* are broader and lower than those on specimens of the round-shouldered early Miocene *M. sula* and have narrower interspaces.

The types of *Misifulgur montemarensis* were found in shoreface sandstone on the lee side of a granitic paleo-island – Montemar. A late Miocene age is inferred from 8-Ma ^{40}K-^{40}Ar-dated ash beds lower in the section (Muizon and DeVries, 1985). Other specimens (MUSM INV 201, MUSM INV 202) were found near Nazca on the lee side of a paleo-peninsula (Cerro Huaricangana; see DeVries, 1988) in littoral sandstones 20 meters above an ash bed (DV 528-1Snee) with a late Miocene ^{40}Ar-^{39}Ar date of 7.51 ± 0.05 Ma (L. Snee, written communications, 1987).

DISCUSSION

Misifulgur dockeryi is the oldest species of its genus by ten million years, so it might be that the Gulf of Mexico, home to other Paleogene buccinoids (MacNeil and Dockery, 1984), was home to the first *Misifulgur*. By the latest Oligocene or earliest Miocene, when no physical barrier had yet separated the Pacific and Atlantic Oceans (Collins et al., 1996), *M. sula* and *M. cruziana* had become established in southwestern Ecuador, northwestern Peru (Olsson, 1931, 1932), and for the latter species, south-central Peru. A similar pattern of distribution characterized the Caribbean genus, *Muracypraea* Woodring, 1957, for which early Miocene northern and southern Peruvian species constituted southern hemispheric outliers (DeVries et al., 2006).

A case against dispersal and in favor of convergence of the Miocene western South American species with an unrelated Gulf Coast Oligocene species could be made based on the absence of Central American records for *Misifulgur*. The buccinids herein referred to *Misifulgur*, however, are rare in northern Peru (three specimens) and southwestern Ecuador (two specimens), indicating that their absence in Miocene deposits of Central America may reflect a Miocene scarcity of individuals or a modern scarcity of preserved paleo-habitat. The issue of convergence versus dispersal will not be resolved until *Misifulgur* is found in Central America or a plausible Oligocene ancestral buccinid is found in western South America.

HISTORICAL BIOGEOGRAPHICAL CONTEXT FOR BUCCINIDS ON THE PERUVIAN SHELF

The modern Peruvian Faunal Province (Dall, 1909; Tarazona et al., 2003), which includes the present-day coastline of the East Pisco and Sacaco basins but not the Talara nor Progreso basins, is inhabited at intertidal and shallow subtidal depths by medium-sized carnivorous muricid gastropods of the genera *Acanthina*, *Concholepas* Lamarck, 1801, *Stramonita* Schumacher, 1817, and *Xanthochorus* Fischer, 1884 (Alamo and Valdivieso, 1997; Guzmán et al., 1998). At inner shelf depths, *Stramonita* and *Xanthochorus* occur together with the carnivorous / scavenging buccinid, *Solenosteira fusiformis* and, off southern Peru, the buccinid, *Aeneator fontainei*, the former with a distribution northward into the Panamic Faunal Province and the latter with southern ocean affinities (Laudien et al., 2007; Araya, 2013; S.V. Mogollón, written communication, 2008). On the Chilean shelf, gastropod

predators include members of the muricid genus *Trophon* Montfort, 1810, the muricid *Chorus giganteus* (Lesson, 1831) (McLean and Andrade, 1982; Gajardo et al., 2002), and *A. fontainei.*

During the early to late Pliocene, soft-bottom substrates of the Peruvian Faunal Province at comparable shallow depths were occupied by the same genera of medium-sized muricids as would be present during the Quaternary, although usually the genera were represented by species now extinct (DeVries, 1995; 2000; 2003; 2005a). Some muricid genera (*Concholepas, Chorus, Trophon, Xanthochorus*) had more expansive distributions, ranging from Chile to Cabo Blanco, northern Peru (Herm, 1969; DeVries, 1986; 1995; 1997; 2005b; 2007a).

From the latest Oligocene to the early late Miocene, *Misifulgur,* especially *M. cruziana,* is inferred from its abundance to have been the predominant medium-sized to large carnivorous neogastropod on the Peruvian shelf. Muricids were rare and small (DeVries, 2005b). A variety of neogastropods inhabited Miocene shelf substrates of Ecuador's Progreso Basin, according to Marks (1951), including *Misifulgur, Conus* spp., *Terebra* spp., and turrids, but notably not muricids. During the late Miocene, the youngest species of *Misifulgur, M. montemarensis,* appeared at inner shelf depths along the southern Peruvian coast, and then, at about 6 Ma, became extinct, an event approximately coinciding with the northward expanding range of a similarly sized, shelf-dwelling, carnivorous neogastropod, the Chilean muricid, *Chorus frassinetti* DeVries, 1997, as well as the appearance of the smaller Peruvian trophinines, *Xanthochorus stephanicus* DeVries, 2005 and *X. ochuroma* DeVries, 2005 (DeVries, 2005a).

CONCLUSIONS

Buccinids in *Misifulgur* new genus probably evolved along the Gulf Coast of the United States during the Oligocene. *Misifulgur* did not experience the same Neogene diversification in the Atlantic realm as other buccinid genera, but before the latest Oligocene evidently passed into the tropical eastern Pacific Ocean, where populations found a niche on soft substrates of the continental shelf from southwestern Ecuador to southern Peru. *Misifulgur cruziana* became the most abundant and perhaps largest carnivorous gastropod inhabiting the southern Peruvian sandy inner shelf during the early and middle Miocene. By the late Miocene, only *M. montemarensis* new species remained, living close to the shoreline on protected sandy substrates. The demise of *M. montemarensis* and thereby the extinction of *Misifulgur* coincided with the late Miocene to early Pliocene advent and diversification of the morphologically similar, shelf-dwelling, carnivorous muricid genus, *Chorus,* as well as the trophinine genus, *Xanthochorus.*

ACKNOWLEDGMENTS

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APPENDIX

Locality numbers of the Burke Museum of Natural History and Culture (Bxxxx), and corresponding DeVries locality-sample numbers (DV xxxx-xx). dep. seq. = depositional sequence.

B8305, DV 377-3	SW wall of Quebrada Gramonal, near juncture with Río Ica; deltaic foresets and bottom-sets of coarse-grained sandstone. 14°45′45″ S, 75°30′27″ W. Chilcatay dep. seq., upper lower Miocene.
B8313, DV 420-1	S end of Filudo Depression; gray sandstone beds. 13°53′12″ S, 76°07′15″ W. Pisco dep. seq., middle Miocene.
B8316, DV 482-8	As for B8316, middle horizon of fossils.
B8333, DV 1320-1	Pampa Colorado, along road to Playa Peñon, indurated red sandstones. 14°25′59″ S, 75°49′19″ W. Pisco dep. seq., lower upper Miocene.
B8343, DV 3004-1	NW corner of Cerro Submarino, above unconformity. 14°34′36″ S, 75°39′55″ W. Lower Pisco dep. seq., middle Miocene.
B8358, DV 395-12	Two km W of Cerro La Virgen, north side of Comotrana-Carhuas road. 14°10′04″ S, 76°07′05″ W. Chilcatay dep. seq., lower Miocene.
B8359, DV 421a-1	N wall of Quebrada Huaricangana, across from small canyons on S wall. 14°57′08″ S, 75°18′06″ W. Pisco dep. seq., upper Miocene.

BS360, DV 430-1 Montemar, three km S of Lomas intersection; shell-rich bed near Panamerican Highway. 15°31'08" S, 74°48'43" W. Pisco dep. seq., upper Miocene.

BS361, DV 441-14 Lower part of measured type section of Chilcatay Formation, 90.8 meters above measured base, "skull horizon." 14°11'31" S, 76°06'56" W. Lower Chilcatay dep. seq., lower Miocene.

BS362, DV 451-2 W side of Filudo depression; anadarid-bearing coarse-grained sandstone bed at 21 meters in measured section. 13°57'19" S, 76°07'19" W. Lower Pisco dep. seq., middle Miocene.

BS363, DV 482-7 Bowl between Cerro La Brujita and Cerro La Bruja on W side Río Ica valley; lowest continuous shell level, with large gastropods. 14°30'41" S, 75°40'00" W. Pisco dep. seq., upper middle Miocene.

BS364, DV 482-10 As for BS316, two meters above middle shell bed.

BS365, DV 484-6 Yesera de Amara, ledges and sandstone horizons on lower NE slopes of buttes. 14°35'38" S, 75°40'10" W. Lower Chilcatay dep. seq., uppermost Oligocene to lower Miocene.

BS366, DV 494-1 Cerro Blanco on W side Río Ica. Mollusks 15 meters above base of measured section, five meters below disconformity. 14°25'22" S, 75°41'12" W. Pisco dep. seq., upper Miocene.

BS367, DV 528-3 S wall of Quebrada Huaricangana, third gulch from W; 40 meters above base of section near E ridge. Shell bed with diverse fauna. 14°57'47" S, 75°16'58" W. Pisco dep. seq., upper Miocene.

BS368, DV 536-1 S wall of Quebrada Huaricangana, 25 meters above base of exposed section; cross-bedded sandstone with scattered *in situ* mollusks. 14°57'11" S, 75°17'08" W. Pisco dep. seq., upper Miocene.

BS369, DV 573-3 Faulted slopes about 1–2 km E of Fundo Santa Rosa, massive sandstone with fish scales. 14°47'16" S, 75°30'22" W. Pisco dep. seq., middle Miocene.

BS370, DV 576-6 Slopes E of Quebrada Gramonal. 14°45'38"S, 75°30'21"W. Pisco dep. seq., lower upper Miocene.

BS371, DV 579-1 South of Quebrada Gramonal, one km E of double-knobbed hill above Río Ica in faulted zone of basement blocks and *Turritella*-sandstone; bed just above marine mammal level. 14°46'30" S, 75°30'06" W. Pisco dep. seq., middle Miocene.

BS372, DV 580-1 1.5 to two km ENE of BS371; white bed with mollusks. 14°46'55" S, 75°29'28" W. Pisco dep. seq., middle Miocene.

BS373, DV 1348-1 E side of Montemar, near Panamerican Highway. 15°31'18" S, 74°48'57" W. GPS. Pisco dep. seq., upper Miocene.

BS374, DV 1403-1 Slope E of Cerro Sombrero, 5 meters above angular unconformity. 14°05'49" S, 76°11'08" W. Basal Chilcatay dep. seq., uppermost Oligocene.

BS375, DV 1611-3 Campsite at Ullujaya West, bowl-shaped depression. 14°34'52" S, 75°38'40" W. Lower Chilcatay dep. seq., uppermost Oligocene.

BS376, DV 1648-1 Valley SW of Cerro Colorado; southwest-facing flank. 14°22'25" S, 75°53'52" W. Chilcatay dep. seq., lower Miocene.

BS377, DV 2005-1 SE side of Laguna Seca, near top of hill, above tuffaceous white horizon. 14°33'28" S, 75°32'46" W. Pisco dep. seq., lower upper Miocene.

BS378, DV 2241-1 SE of Cerros Colorados, edge of tilted surface of alluvial boulders with W source. 14°22'46" S, 75°53'50" W. Lower Chilcatay dep. seq., uppermost Oligocene to early Miocene.

BS379, DV 4076-1 SE Cerros Colorado, above angular unconformity. 14°22'55" S, 75°53'52" W. Lower Chilcatay dep. seq., uppermost Oligocene.

DV 494-5Snee As for BS366, but 82 m above base of measured section, ash bed, 6.85 ± 0.07 Ma. No Burke locality number.

DV 528-1Snee As for BS367, but 20 m above base of measured section, ash bed, 7.51 ± 0.05 Ma. No Burke locality number.

A new species of *Admete* (Gastropoda: Cancellariidae: Admetinae) from the Paleocene of eastern Hokkaido, northern Japan

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ABSTRACT

A new cancellariid species, *Admete katsuhiraensis* new species is described from the Paleocene Katsuhira Formation in Urahoro Town, eastern Hokkaido, Japan. This is the oldest record of cancellariid gastropods in Japan and also the oldest record of the genus *Admete* and the subfamily Admetinae worldwide. Although the known fossil record of the genus is very incomplete, occurrence of Paleocene Admetinae in deep sea deposits of the Katsuhira Formation in northern Japan provides an interesting insight into the timing of origin of the present day cold water molluscan fauna in the northern Hemisphere.

INTRODUCTION

Cancellariids consist of a diverse group of mostly warm-water mollusks. Biodiversity estimates for Cancellariidae include 1200 fossil and 300 recent species (Hemmen, 2007), and 124 genera and 1864 recent and fossil species, according to Petit and Harasewych (2005). The oldest geological records of the family date from the Late Cretaceous (Cenomanian) of Texas and the family reached its maximum diversity in the Eocene and Miocene (Stephensen, 1952; Taylor and Morris, 1988; Hemmen, 2007). No Cretaceous cancellariids have been recorded from Japan (see Hayami and Kase, 1977; Kase, 2001). The oldest species from Japan are *Cancellaria*? sp. indet. a, b, c, d from the upper Eocene Kyuragi and Kijima Formations and the lower Oligocene Yamaga Formation in northern Kyushu (Nagao, 1928). However, columellar folding, one of the distinct characteristics of cancellariids, has not been recognized on those Eocene species from Kyushu. These Paleogene species from Kyushu were reexamined by Oyama et al. (1960), and *C.*? sp. indet. a, b from the upper Oligocene Yamaga Formation were reassigned to *Trigonostoma*? (*Scalptia*?) sp. No Paleogene cancellariids have been recorded in Sakhalin, while several cancellariid species have been described and illustrated from the Paleogene deposits of western Kamchatka (Gladenkov et al., 1991).

Specimens of a small cancellariid have been recently collected from the Paleocene (Danian–Selandian) Katsuhira Formation (see Amano and Jenkins, 2014) in eastern Hokkaido. In this paper, we describe these as a new species and discuss its biogeographic significance.

MATERIALS AND METHODS

Two specimens of cancellariid gastropods were collected from dark gray mudstone of the upper part of Katsuhira Formation at the cliff along Urahoro River near Katsuhira, Urahoro Town, eastern Hokkaido (Figure 1). The age of the formation was assigned to the Paleocene (Danian–Selandian), based on the planktonic foraminifera and calcareous nannofossils (Kiminami et al., 1978; Kaiho, 1984; see also Amano and Jenkins, 2014).

Cancellariid specimens from this locality are associated with protobranch bivalves such as *Acila, Leionucula, Malletia,* and deep-sea arcid *Bentharca steffeni* Amano, Jenkins and Nishida, 2015. Although paleoenvironments of the Katsuhira Formation have not been studied in detail, these bivalves indicate deposition in deep water (Amano and Jenkins, 2014; Amano and Oleinik, 2014; Amano et al., 2015). One institutional acronym used is: JUE, Joetsu University of Education, Joetsu, Niigata Prefecture.

SYSTEMATIC PALEONTOLOGY

Class Gastropoda Cuvier, 1797
Order Neogastropoda Wenz, 1938
Superfamily Cancellarioidea Forbes and Hanley, 1851
Family Cancellariidae Forbes and Hanley, 1851
Subfamily Admetinae Troschel, 1865

Remarks: Admetinae is characterized by thin shell and columella with arched and weak columellar folds (Wilson, 1994). Recent molecular phylogeny work reveals that this subfamily, as it is now understood, is polyphyletic (Modica et al., 2011). The genus *Admetula*
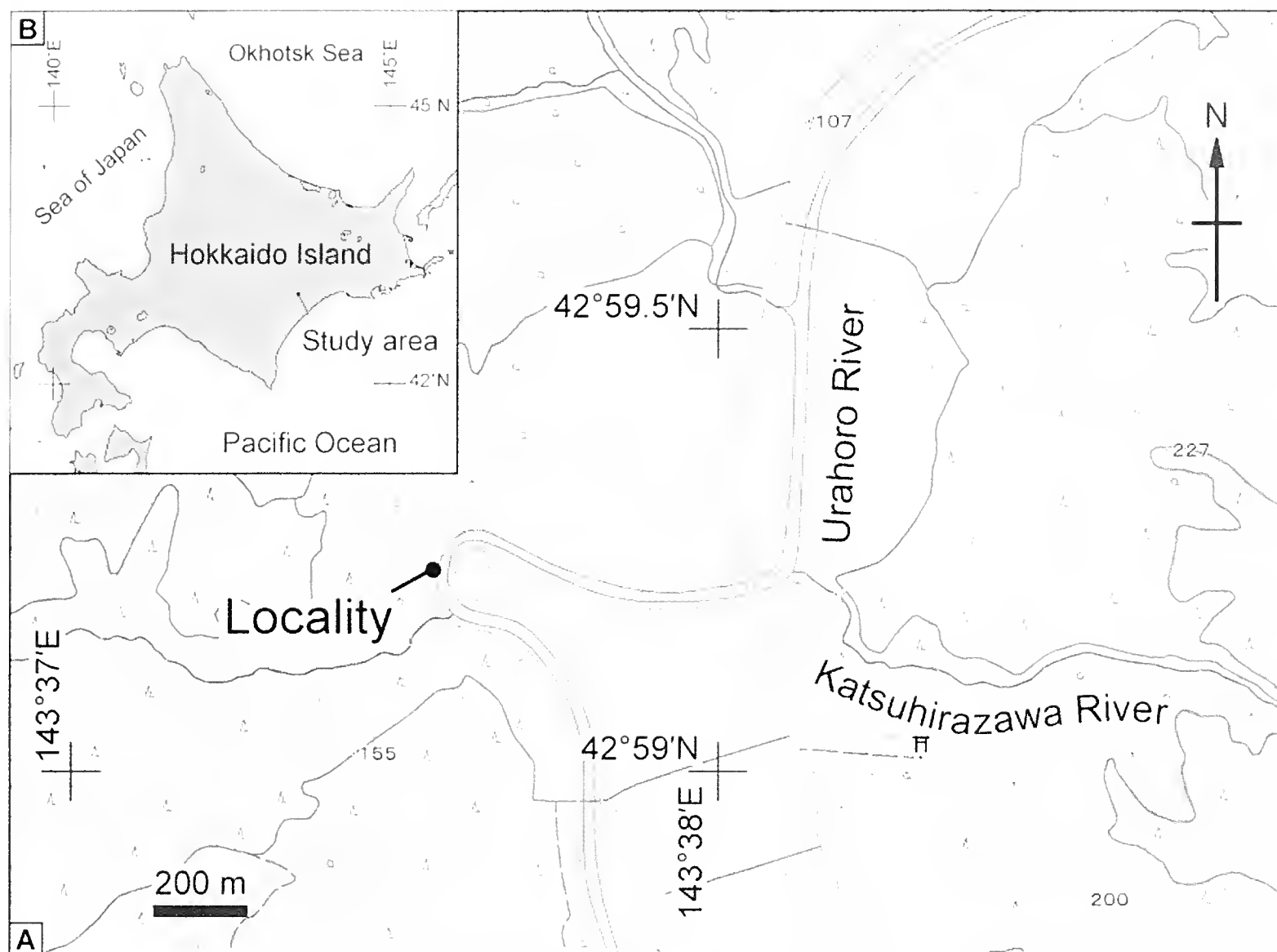
Figure 1. Locality map of *Admete katsuhiraensis* new species. (Base map is from "Katsuhira", scale 1: 25,000; topographical map published by the Geospatial Information Authority of Japan).

Cossmann, 1899 is considered as a separate from Admetinae clade. This classification was used by Harzhauser and Landau (2012) when they revised the Neogene cancellariids of the Paratethys. They also treated *Bonellitia* Jousseaume, 1887 as the *Admetula* clade, despite of lack of molecular data.

Genus *Admete* Krøyer in Möller, 1842

Type Species: *Admete crispa* Möller, 1842 (= *Tritonium viriduhm* Fabricius, 1780) by monotypy.

Remarks: The genus *Admete* is characterized by a rather thin shell with large last whorl, deep sutural groove, narrow shoulder and by having a straight collumella with two weak folds and narrow umbilicus or slit (Harasewych and Petit, 1986: 86; this study). *Neadmete* Habe, 1961 can be separated from the genus *Admete* by having a higher spire and rather straight collumella with three folds. *Zeadmete* Finlay, 1926 differs from *Admete* by a fine cancellate sculpture on entire

surface. Genera *Admetula* and *Bonellitia* have a thick crenulated outer lip, three strong columellar folds and lack umbilicus or slit. The American Cretaceous genus *Admetopsis* Meek, 1873 including *Admete*? *gregaria* Meek, 1873, *A.*? *subfusiformis* and *A.*? *rhomboides* Meek, 1873 can be clearly separated from *Admete* by having rounded whorls without shoulder, a significantly higher spire, an anteriorly thickened calcareous callus, by weaker or absent of collumellar folds, and lack of an umbilicus or slit. It is presently not clear if *Admetopsis* belongs to Admetinae or not. Another American Cretaceous genus *Paladmete* Gardner, 1916 can be easily distinguished from *Admete* by having a smooth collumella without folds. Stephenson (1941) established family Paladmetidae based on this genus.

Admete katsuhiraensis new species
(Japanese vernacular name: Katsuhira-koromogai)
(Figures 2, 3)

Diagnosis: Shell small with cancellate sculpture consisting of 15 to 21 spiral cords and 19 to 23 axial ribs.
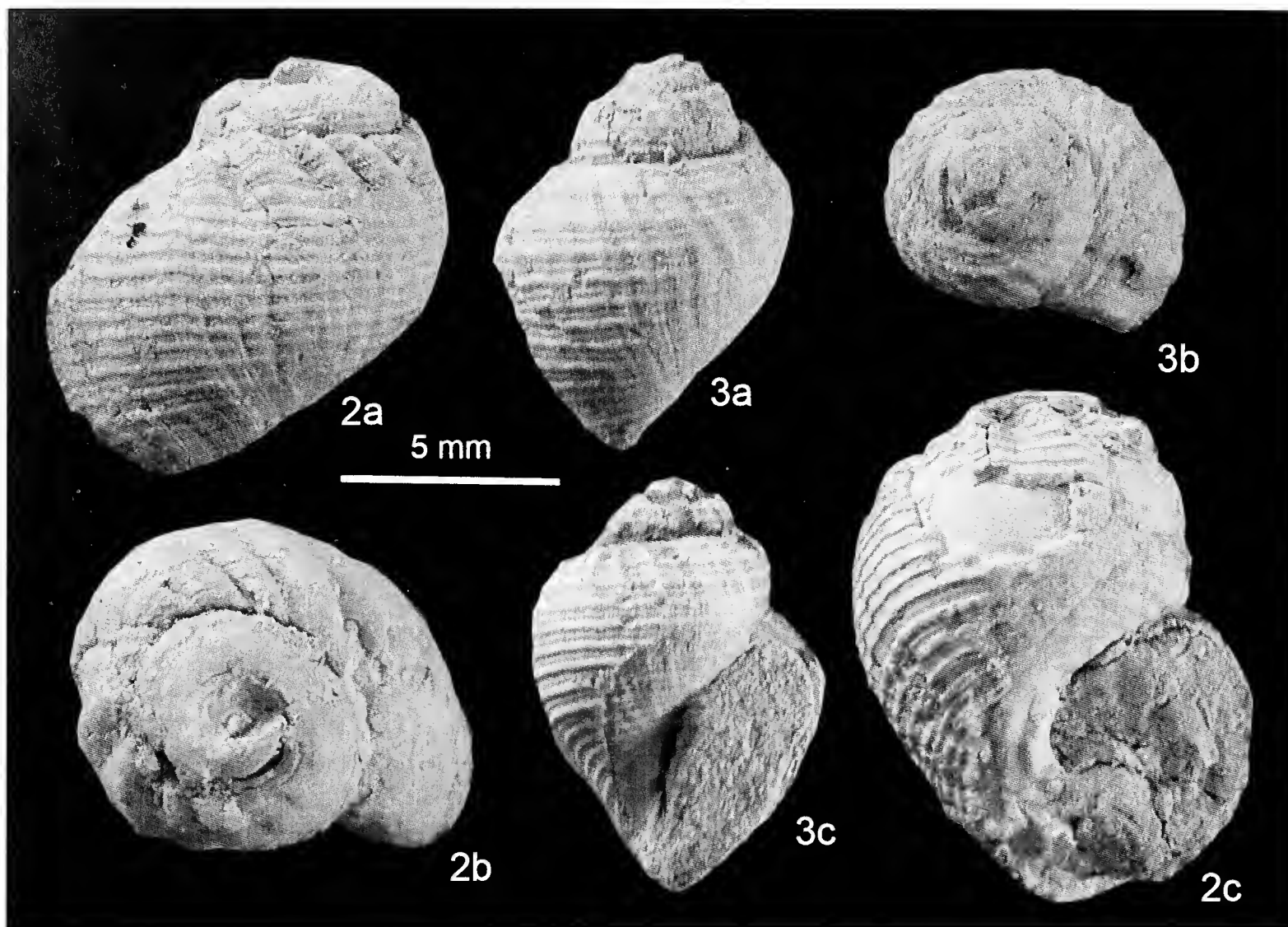
Figures 2, 3. *Admete katsuhiraensis* new species. **2**. Paratype, JUE no. 15940; **2a**, adapertural view; **2b**, apical view; **2c**, apertural view. **3**. Holotype, JUE no. 15939; **3a**, apical view; **3b**, adapertural view; **3c**, apertural view.

Four whorls with rather deep sutural groove; spire low, 1/8 of shell height. Columella nearly straight with two weak folds; inner lip broadly covered by thin calcareous callus; siphonal canal short with very weak fasciole and very narrow umbilical slit.

Description: Shell small, attaining 11.4 mm in height, thin, fusiform, with four whorls. Sutural groove rather deep; very narrow shoulder present in holotype. Last whorl large, occupying approximately 7/8 of the height of shell; spire very low; protoconch poorly preserved, half of smooth volution remaining. Surface of last whorl sculptured by 19 to 23 rounded axial ribs that become obsolete toward base, separated by equal or narrower interspaces, more distinct near suture. Spiral sculpture of last whorl consisting of 15 to 21 flat cords sometimes with one weak cord in between. Sculpture of penultimate whorl consisting of 20 fine axial ribs and five spiral cords in holotype. Outer lip thin and not crenulated; columella nearly straight with two weak folds; inner lip broadly covered by thin calcareous callus; siphonal canal short with very weak fasciole and very narrow umbilical slit recognized in paratype specimen.

Type Material: Holotype, JUE no. 15939 (Shell height, 8.0 mm; Diameter, 6.0 mm); Paratype, JUE no. 15940 (Shell height, 11.4 mm; Diameter, 9.9 mm)

Type Locality: The cliff along Urahoro River at 750 m downstream from the mouth of Katsuhirazawa River, Urahoro Town, eastern Hokkaido. Danian to Selandian Katsuhira Formation.

Remarks: *Admete viridula* (Fabricius, 1780) is the only species of *Admete* recorded from the upper Miocene to Pleistocene deposits in Japan as *A. couthouyi* (Jay, 1839) (Amano, 1983; Baba, 1990). According to Sneli and Stockland (1986), the latter name is a junior synonym of *A. viridula*. This species differs from *A. katsuhiraensis* new species by its larger size (more than 20 mm in height), a rounded shoulder, very faint columellar plaits and more strongly curved columella.

Admete katsuhiraensis new species is similar to *Admete profundicola* (Okutani, 1964) which lives at 1500 m depth off Sagami Bay, central Honshu. Both species share small shell size (*A. profundicola*; shell height, 7.8 mm; diameter, 5.0 mm), angulated shoulder,

very narrow umbilicus, two columellar folds and similar number of spiral cords (15 in the last whorl of *A. profundicola*). The new species is different from *A. profundicola* in having a lower spire and more numerous axial ribs (17–19 in the last whorl of *A. profundicola*).

The new species resembles *A. californica* Dall, 1908 (found around 1103 meters in the Gulf of California) by having a similar number of spiral cords and axial ribs (both 20 in the last whorl of *A. californica*). However, the new species can be separated from *A. californica* by having a larger shell (16 mm in height of *A. californica*), lower spire and very narrow umbilical split.

The new species differs from the Miocene *A. kamtschatica* Sinelnikova in Gladenkov and Sinelnikova, 1990 from the Ilyinskaya Formation, western Kamchatka by its smaller size, more compressed shell, with less whorls, a more inflated and larger (7/8 of the total shell height) last whorl, and a deep sutural groove.

Cancellaria globulosa Holzapfel, 1888, from the Cretaceous of western Germany, has a similar outline of shell and two columellar folds. However, it differs from the new species by its thick shell with multiple crenulations inside the outer lip, lack of a deep suture, and lack of an umbilical slit.

Etymology: The new species is named for the location where the type material was collected.

Distribution: Known only from the type locality, Paleocene Katsuhira Formation, Danian to Selandian, Urahoro Town, eastern Hokkaido.

DISCUSSION

The oldest fossil specimens identified as *Admete*? were recorded from the Cretaceous in North America. However, as noted above, these species belong to a distinct genus, *Admetopsis*. *Admete (Bonellitia) funigera* described by Staadt in Cossmann, 1913 (202–203, pl. 7, figs 212–9), from the Paleocene of France, possesses strong collumella folds, and lack a sutural groove and umbilical slit. These morphologic features suggest that *A. funigera* should be classified as *Bonellitia* as was originally proposed by the author. Kollmann and Peel (1983: 93, fig. 209) described and figured an *Admete* from the Paleocene (Selandian) Sonja Member of the Agatdal Formation in central Nûgssuaq of western Greenland. Schnetler and Petit (2010: 22) reexamined these gastropods and allocated that species to *Eocantharus* Clark, 1938 (family Buccinidae). One more species of *Admete* was recorded from the Paleocene (early Selandian) of Greensand at Sundkrogen, Copenhagen, Denmark. The following species from these deposits were described as *Cancellaria* by von Koenen (1885: 8–12): *C. latesulcata, C. conoidea, C. tricarinata,* and *C. curta*; Ravn (1939) placed them in "*Admete*?." However, the former three species were later allocated respectively to *Admetula, Kroisbachia* and *Brocchinia* by Schnetler (2001). Although that author eliminated the question mark from *A.? curta*, it is difficult to decide whether to allocate it to *Admete* because of its very small shell size (3.7 mm; Ravn, 1939: 86, pl. 3, figs 20a, b) and relatively large protoconch, indicative of a juvenile individual. The genera *Kroisbachia, Brocchinia, Admetula,* and *Unitas* are known from the lower Paleocene (Luzanovka beds) of Ukraine (Makarenko, 1976). *Bonellitia (Admetula) paucivaricata* (Gabb, 1864) was illustrated from the Paleocene (Danian) Getkilninskaya Formation by Gladenkov et al. (1997: pl. 33, fig. 33). *Admete ornata* Ilyina, 1955 was described from the Paleogene of the Ustiurt region (vicinity of the Aral Sea) (Ilyina, 1955: 78, pl. 30, fig. 16). However, that species has strong axial ribs and lack sutural groove which is not characteristic of the genus *Admete*. Although the family Cancellariidae is present in the Paleocene deposits of Europe, Greenland and Kamchatka, no proven records of the subfamily Admetinae are known to date from Paleogene deposits anywhere in the world. Thus, *Admete katsuhiraensis* new species from the Danian to Selandian Katsuhira Formation is not only the oldest record of cancellariid in Japan, but also constitutes the oldest record of the genus *Admete* and the subfamily Admetinae.

The genus *Admete* Krøyer in Möller, 1842, today is restricted to cold waters and considered to be an Arcto-Boreal taxon (Kantor and Sysoev, 2006; Thorson, 1944; Macpherson, 1971; Golikov and Scarlato, 1977; Golikov, 1995; Golikov and Sirenko, 1998, 2004; Gulbin, 2004). Occurrences of the genus *Admete* in the Southern Hemisphere and subantarctic waters (Powell, 1951, 1958; Knudsen, 1964) have yet to be investigated. Some of these have been already reassigned to different genera, the taxonomic status of other species have to be adjusted after the study of soft parts morphology. Arctic and Antarctic mollusks are well known for the convergence in shell morphology, which makes their identification based on the shell morphology alone uncertain at best.

Paleocene marine isotopic records do not indicate a significant departure in sea-surface temperature values from the Late Cretaceous and do not indicate the existence of a significant thermocline (Bralower et al., 2002; Dutton et al., 2005), but there are some indications of warm global temperatures (Adatte et al., 2002) during the early Paleocene. These paleoceanographic conditions, coupled with continuous extended shallow shelf around the rim of the North Pacific, facilitated the dispersal of molluscan faunas, which resulted in general similarity between the northeastern and northwestern Pacific Paleocene molluscan faunas. The majority of faunas appears to be of warm to warm-temperate affinities (Oleinik, 2001), lacking cold-water taxa found in the North Pacific today. Fauna of the Katsuhira Formation, which was previously virtually unknown, shows a departure from this general pattern in having a very high degree of endemism and the appearance of new genera, such as the buccinid *Urahorosphaera* (Amano and Oleinik, 2014), new species such as the aporrhaid, *Kangillioptera inoui* (Amano and Jenkins, 2014), or the first appearance of the modern day cold water genus *Admete* described herein. Since there are no true Paleocene *Admete* species or even

subfamily Admetinae records anywhere in the northern hemisphere, the occurrence of *Admete katsuhiraensis* new species has interesting implications on the history of the formation of cold water molluscan faunas known today in the Arctic and boreal regions. As noted above, the lithology and faunal assemblage of the Katsuhira Formation, from which *Admete katsuhiraensis* new species was found, are indicative of relatively deep water deposits. That not only makes this locality unique among the North Pacific shallow-marine Paleocene deposits, but also may suggest a deep water origin of some modern day Arcto-Boreal taxa in the early part of the Paleogene in the North Pacific.

ACKNOWLEDGMENTS

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Hesperaptyxis, a new genus for some western American Fasciolariidae (Gastropoda), with the description of a new species

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ABSTRACT

Hesperaptyxis is proposed as a new genus for *Turbinella cinerea* Reeve, 1847 and five other species from southern California and northwestern Mexico, including the new species *H. negusi*. It differs from *Aptyxis* Troschel, 1868 (Late Miocene to Recent, Mediterranean and temperate eastern Atlantic) by having a slightly upturned siphon and completely adherent inner lip. It differs from the Late Miocene western Atlantic genus *Pseudaptyxis* Petuch, 1988 by much more prominent axial and spiral sculpture and by lacking adapical and abapical sinuses on the outer lip. *Hesperaptyxis* is so far known fossil only from the Pliocene and Pleistocene.

Additional Keywords: Mollusca, Miocene, Pliocene, Pleistocene, recent, Baja California

INTRODUCTION

The classification of members of *Fusinus* Rafinesque, 1815 and related genera has long presented problems. Until recently, most species have been placed in the overly broad genus *Fusinus*. It has become clear, however, that although *Fusinus* and related genera form a clade, which Couto and colleagues (2016) call the *Fusinus colus* clade, there is substantial diversity in this group. Most attention has been focused on large-shelled species, leaving small-shelled taxa underrepresented in most recent studies. Russo (2015) treated the taxon *Aptyxis* Troschel, 1868, a member of the *F. colus* clade (Couto *et al.*, 2016), assigning to it *Murex syracusanus* Linnaeus, 1758 (the type species, from the Mediterranean Sea and adjacent warm-temperate eastern Atlantic) and the Californian *Fusus luteopictus* Dall, 1877. Russo (2015) failed to note that Abbott (1954: 244) had previously assigned *Fusus luteopictus* to *Aptyxis*, and Keen (1958: 617–618) had assigned two additional eastern Pacific species, *Turbinella cinerea* Reeve, 1847 and *Fusinus felipensis* Lowe, 1935, to *Aptyxis*. Keen (1971) left the somewhat larger eastern Pacific *Fusinus*

fredbakeri Lowe, 1935, in *Fusinus* sensu lato. No adequate description of *Aptyxis* has appeared to date, rendering generic assignments arbitrary at best. Our purpose in this article is to characterize these small species, to propose the new genus *Hesperaptyxis* for the small eastern Pacific species, to describe the new species *H. negusi* from Baja California, and to discuss the biogeographic conundrum presented by small northern-hemisphere fusinine fasciolariids. An institutional acronyms is: ANSP, Academy of Natural Sciences of Drexel University, Philadelphia, PA.

SYSTEMATICS

Family Fasciolariidae Gray, 1853
Subfamily Fusininae Wrigley, 1927

Genus *Hesperaptyxis* new genus

Type Species: *Turbinella cinerea* Reeve, 1847, designated herein (Recent, northwestern Mexico; Pliocene, Isla Carmen [Gulf of California, Baja California Sur State], Mexico; Pleistocene, Isla Coronados [Gulf of California Baja California Sur state], Mexico) (Figures 1, 2, 22)

Diagnosis: Small fusinine fasciolariids with angulated shoulder cord, convex outer lip, distinct abapical and adapical sinuses on the outer lip, and siphon with slightly upturned tip and inner lip adherent throughout its length.

Description: Shell small, maximum length about 70 mm, fusiform. Protoconch paucispiral. Teleoconch with up to 8 whorls. Suture accentuated by steep subsutural slope on all whorls. Teleoconch sculpture consisting of strong spiral cords and axial ribs. Shoulder cord angulated. Central cord at adapical end of base less prominent. Base strongly constricted. Spiral cords present on entire siphon. Tip of siphon slightly upturned (Figure 22). Aperture elongate-ovate. Outer lip crenulated at edge, smooth or weakly lirate within. Inner lip
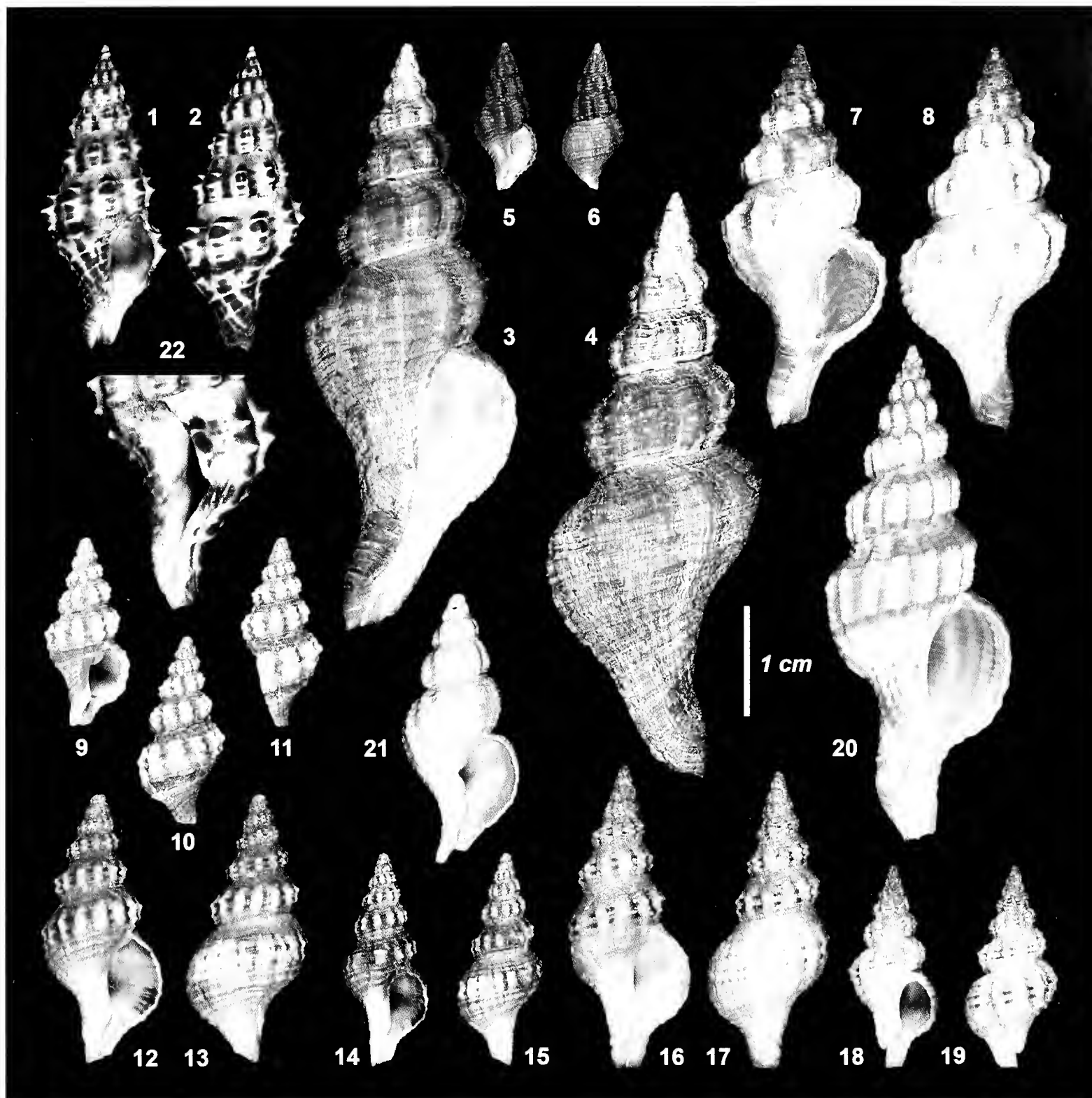
Figures 1–22. **1, 2.** *Hesperaptyxis cinereus* (Reeve, 1847). ANSP 466447, off La Paz, Gulf of California, Baja California Sur, Mexico, 1992, 28.3 mm. **3, 4.** *Hesperaptyxis ambustus* (Gould, 1853). ANSP 466448, off Guaymas, Gulf of California, Sonora, Mexico, 1955, 54.9 mm. **5, 6.** *Hesperaptyxis felipensis* (Lowe, 1935). ANSP 466449, on underside of rocks as low tide, Puertecitos, Gulf of California, Baja California Norte, Mexico, 1985, 13.9 mm. **7, 8.** *Hesperaptyxis fredbakeri* (Lowe, 1935). 36.0 mm, live from Cholla Bay, Puerto Penasco, Gulf of California, Sonora, Mexico, ANSP 466450. **9–15.** *Hesperaptyxis luteopictus* (Dall, 1877). **9–11.** USNM 32350, Monterey, California., 17.5 mm. **12–15.** On rocks by Scuba at 6–9 m, Santa Cruz Island off Santa Barbara, California, 21.0 mm, 25.1 mm, **16–19.** *Hesperaptyxis negusi* new species. **16–17. Holotype,** ANSP 466446, live on rocks at 12–24 m, San Bonito Island [west of Cedros Island], Pacific Baja California, Mexico, 28.6 mm. **18–19. Paratype,** ANSP 466445, from type locality, 19.1 mm. **20.** *Aptyxis syracusanus* (Linnaeus, 1758). ANSP 466452, off southern Sicily, 1955 m, 46.6 mm. **21.** *Pseudaptyxis santamariae* Petuch, 1988. ANSP 52871, late Miocene (Turtonian) St. Mary's Formation, Maryland, 26 mm. **22.** *Hesperaptyxis cinereus* (Reeve, 1847). ANSP 466447, 28.3 mm, off La Paz, Gulf of California, Baja California Sur, Mexico, 1992, anterior part of shell, 28.3 mm.

smooth, columellar margin resorbed in posterior third, callused and slightly produced in anterior third, with transition between (Figure 22). Single entrance fold at base of siphonal canal, shallow abapical sinus present on outer lip, aperture slightly folded at terminus of suture.

Included Species: *Turbinella cinerea* Reeve, 1847 (Figures 1, 2); *Fusus ambustus* Gould, 1853 (Figures 3, 4); *Fusinus felipensis* Lowe, 1935 (Figures 5, 6); *Fusinus fredbakeri* Lowe, 1935 (Figures 7, 8); *Fusus luteopictus* Dall, 1877 (Figures 9–15); *Hesperaptyxis negusi* new species (Figures 16–19). (The upturned canal tip was previously noted for *Fusinus fredbakeri* by Hertz et al. (1999: 80, table 2): [canal] "tip bent to left".)

Etymology: Combination of *Hesperia* (Greek, land to the west) and *Aptyxis*.

Comparisons: In shell characters, *Hesperaptyxis* is extremely similar to *Aptyxis* Troschel, 1868, type species *Murex syracusanus* Linnaeus, 1758, from the Mediterranean Sea and adjacent warm-temperate eastern Atlantic. Although there have been occasional placements of additional Mediterranean species in *Aptyxis*, we are basing our comparison on the type species, *Murex syracusanus* (Figure 20). The genus *Aptyxis* differs from *Hesperaptyxis* by having a straight siphon without upturned tip and by having the abapical end of the inner lip, at the distal end of the siphonal canal, forming a detached edge to the left margin of the canal. This occurs in roughly 50% of mature specimens (n=12).

Another similar genus is *Pseudaptyxis* Petuch, 1988, based on *P. santamariae* Petuch, 1988 from the Late Miocene (Tortonian) St. Mary's Formation of Maryland. Our examination of the holotype of *P. santamariae* (ANSP 52871) (Figure 21) shows that this small species (length about 25 mm) differs from both *Aptyxis* and *Hesperaptyxis* by much finer spiral and axial sculpture and by having a straight outer lip without abapical and adapical sinuses. The outer lip is smooth within, and a parietal tooth or ridge is absent. *Pseudaptyxis* resembles *Hesperaptyxis* in having the tip of the siphon slightly upturned. In this respect, *Hesperaptyxis* and *Pseudaptyxis* differ from the eastern Atlantic *Aptyxis*. In addition, the shoulder is rounded in *Pseudaptyxis*, whereas it is more or less angulate in *Aptyxis* and *Hesperaptyxis*.

Hesperaptyxis negusi new species
(Figures 16–19)

Description: Shell small, slender, to about 29 mm, with short siphonal process. Protoconch broken or missing in all specimens examined. Teleoconch of 8 convex whorls at maturity, constricted at sutures. Axial sculpture of about 12 ribs on early and penultimate whorl, 18 on body whorl, morphing on last whorl to weak axial ridges toward lip. Ribs stop short of suture posteriorly and anteriorly. Spiral cords on entire teleoconch, to tip of neck, about 5 on early whorls, 6 on penultimate whorl with intercalated weaker cords; spiral sculpture weaker on body whorl. Anterior sutural ramp steep with strong cord at base, 3–4 close–set cords on ramp. Rounded knobs where spiral cords cross axial ribs, evanescent on second half of body whorl. Siphonal process short, straight, with slightly upturned tip. Aperture elongate-ovate, glazed white within with raised cords terminating short of lip; small entrance fold at base of siphonal canal. Parietal callus resorbed, blending smoothly into exterior shell surface. Columellar margin of siphonal canal raised. Operculum typical of genus, thin, light caramel color. Shell background color pale to light brown. Spiral cords dark brown between axial ribs, cream color at knobs where crossing axial ribs. Remnants of one protoconch suggest a dark caramel color.

Type Material: Holotype (Figures 16–17): ANSP 466446, length 28.6 mm, live on rocks at 12–24 m, 1989; Paratype (Figures 18–19), length 19.1 mm, live on rocks at 12–24 m, ANSP 466445; Both from type locality.

Type Locality: San Benito Island [west of Cedros Island], Baja California State, Mexico.

Etymology: Named for Rick Negus, who recognized the taxon as an unnamed species and donated the holotype and paratype.

Distribution: From Santa Cruz Island south to San Benito Island.

Remarks: *Hesperaptyxis negusi* is most closely related to *H. luteopictus*, being of similar size and shape, and sharing the same or similar habitats. It is easily distinguished from *H. luteopictus* by its more slender and elongated profile and its less prominent sculpture. *H. luteopictus* is purplish brown with white spiral bands where prominent centrally placed cords cross raised portions of axial ribs, forming sharply pointed knobs. *H. negusi* has a smoother more rounded surface sculpture.

BIOGEOGRAPHY

Despite their great similarity in shell characters, species of the eastern Atlantic *Aptyxis* and eastern Pacific *Hesperaptyxis* are separated by a large geographic gap. *Aptyxis* has been part of the southern European and eastern Atlantic fauna since at least the Late Miocene and Pliocene (see Landau et al., 2013). *Hesperaptyxis* is known only from fossils from the Pliocene and Pleistocene of the Gulf of California, with records of *H. cinereus* from Isla Carmen (Pliocene; Durham, 1950) and Isla Coronados (Pleistocene; Emerson and Hertlein, 1964). No similar species are known from the rich Neogene faunas of the Caribbean region. Petuch (1988) described *Pseudaptyxis* for the single species *P. santamariae* from the Late Miocene of Maryland. Here again, no similar

taxon is known that might connect this genus phylogenetically with either *Aptyxis* or *Hesperaptyxis*. These biogeographic separation corroborates a taxonomic separation among these three very similar genera.

The restriction of *Hesperaptyxis* to the coasts of southern California and northwestern Mexico has parallels in other molluscan genera. The closest parallel is with the ocenebrine muricid genus *Mexacanthina* Marko and Vermeij, 1999, whose three species are common intertidal gastropods on rocky shores of the Pacific side of Baja California and the Gulf of California. Like *Hesperaptyxis*, *Mexacanthina* has no obvious relatives in the Neogene or Recent fauna either in western North America or elsewhere. It converges in form on the phylogenetically distinct eastern Atlantic genus *Spinucella* Vermeij, 1993 (Early Miocene to Late Pleistocene).

Another geographically restricted genus in the living fauna is *Macron* H. and A. Adams, 1853, with a modern distribution coincident with that of *Hesperaptyxis* and *Mexacanthina*. In this case, however, there are fossil species in the Early Miocene of Venezuela (Gibson-Smith et al., 1997) and the Miocene of Chile (Nielsen and Frassinetti, 2003). Other examples are *Megastraea* McLean, 1970 (Turbinidae), *Liocerithium* Tryon, 1887 (Cerithiidae), *Myrakeena* Harry, 1985 (Ostreidae) and *Austrotrophon* Dall, 1902 (Muricidae: Ocenebrinac). Hypotheses for how these restricted distributions came to be have not been offered, but it is clear from these examples and from *Hesperaptyxis* that the region from southern California to the subtropical coasts of the Gulf of California is geographically unique.

ACKNOWLEDGMENTS

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The western Caribbean complex of *Fasciolaria tephrina* de Souza, 2002 (Gastropoda: Fasciolariidae), with the description of a new species

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ABSTRACT

Fasciolaria delicatissima new species, a capacious, thin-shelled, deep-water fasciolariid from a restricted area of the southwestern Caribbean Sea, is compared with the similar *F. tephrina* de Souza, 2002 and *F. cf. tephrina*, a presumed color form of the latter; all three taxa have paucispiral protoconchs.

Additional Keywords: Southwestern Caribbean Sea, Honduras, Nicaragua, Recent

INTRODUCTION

The molluscan fauna of the western Caribbean was mostly unknown when one of the authors (EFG) began visiting Roatán Island, Bay Islands, Honduras in 1978. Many vessels of the commercially important Honduran shrimp and spiny lobster fisheries land catches at Roatán, and bycatches from those vessels has revealed a remarkable molluscan fauna. Most species caught in shrimp trawls are different than those caught in lobster traps, but both types of collecting gear have produced many indigenous species previously unknown to science. The fauna is so different that Petuch (1988: 62) identified it as one of several "relict pockets" in the Caribbean region. Although Petuch considered the pocket's center to be around the Bay Islands (Utila, Roatán, and Guanaja) just off the Honduran coast, in reality the area comprises the entire wide continental shelf and upper slope that borders the Caribbean coasts of Honduras and Nicaragua (Figure 17). The range of the classic species *Voluta polypleura* Crosse, 1876 roughly defines the boundary of this "pocket."

After a lapse of 15 years, trips to Roatán were resumed in 2012 by EFG. Some previous contacts had lately been working aboard vessels fish-trapping on the Honduran slope seaward of the 100-fathom (183 m) isobath (Figure 17). This activity had yielded species not seen during some 60 previous trips, over a period of 20 years. Of particular interest was the recently described *Fusilaria garciai* Snyder, 2013, a fasciolariid with a paucispiral protoconch that grows to 225 mm and seems to inhabit at least the length of the northern upper continental slope from north of Cabo Camarón, Honduras to the Nicaraguan border. Also of great interest was a presumed color form of the typically white *F. tephrina* de Souza, 2002. Reported as the "splotched" form of *F. tephrina* by Snyder (2013: 128), the form is referred to here as *F. cf. tephrina*. Both the white and the colored form have been collected near the northeastern corner of the continental slope (Figure 17), but only the colored form has been collected with *Fusilaria garciai*.

The type locality for *Fasciolaria tephrina* is north of Quita Sueño Bank, Colombia (off northeastern Nicaragua), 14°40' N, 81°25' W, depth 480 m (de Souza, 2002: Figure 17). However, de Souza also recorded a specimen in the Kevan and Linda Sunderland collection that was taken "off Roatán Isl., Honduras, 420 m, in fish trap." The fact that the Sunderland specimen was collected in a fish trap seems telling. Fishermen who have collected *F. tephrina* and *F. cf. tephrina* report that they are caught in fish traps set off the edge of the continental shelf. The topography of the upper slope in that area is too rough for trawling and probably unattractive to spiny lobsters, which usually live in warmer, shallower waters, perhaps explaining why the area has been avoided by shrimp and lobster fishermen.

Fasciolaria tephrina has also been reported from off Isla de San Andrés, Colombia (e.g., Miloslavich et al., 2010; Snyder, 2013: 128, fig. 14), an island of volcanic origin separated from the continental shelf and located off the southeastern Nicaraguan coast (Figure 17). However, inspection has revealed several shell characters that differentiate the San Andrés population from *F. tephrina*. The San Andrés population is described here as a new species and compared with *F. tephrina* and *F. cf. tephrina*.

MATERIALS AND METHODS

Specimens studied are located at the Museu de Zoologia da Universidade de São Paulo, Brazil (MZSP), the Academy of Natural Sciences of Drexel University, Philadelphia (ANSP), the William G. Lyons study collection (LC) and the author's collection (EFG). Shell sizes are reported in millimeters (mm), measured to nearest 0.1 mm with electronic digital calipers. Unless otherwise specified, measurements are of shell length (height), measured as the distance between the apex and the abapical end of the siphonal canal. Shells were weighed with a Mettler Toledo PB metric scale model PB 3002-S and measured to the nearest 0.01 grams.

SYSTEMATICS

Family Fasciolariidae Gray, 1853

Genus *Fasciolaria* Lamarck, 1799

Type Species: *Murex tulipa* Linnaeus, 1758, by monotypy.

Fasciolaria delicatissima new species
(Figures 1–7)

Fasciolaria tephrina.—Mallard and Robin, 2005: 8, pl. 4; Robin, 2008: 207, fig. 9; Miloslavich et al., 2010: Table S6, no. 925 (in part); Snyder, 2013: 128, fig. 14 (in part) (*non Fasciolaria tephrina* de Souza (2002), *nec* Snyder (2013: 128, fig. 15)).

Diagnosis: Shell large, capacious, with very thin walls and paucispiral protoconch; shell color off-white with many thin, brown, uneven and sometimes interrupted spiral lines on spire and body whorl; lines not extending onto tan siphonal process.

Description: Shell large, up to 280 mm in length (Rosenberg, 2009), 105 mm wide, fusiform, semi-glossy, with swollen, rounded whorls and uncommonly thin walls. Protoconch (Figure 7) white, large, height approximately 3.5 to 4 mm, smooth, with one whorl; first half of whorl rounded, second half swollen; protoconch axis not deviating from that of teleoconch. Teleoconch with 7 rounded whorls, first two whorls shouldered to periphery, then straight (Figure 7); remaining whorls progressively more convex, body whorl swollen, globose. Suture deep, bordered anteriorly by a strong cord wrinkled by minute axial threads. Axial sculpture of numerous microscopic threads showing at start of teleoconch, approximately 30 on first whorl and 60 on second whorl; axial swelling appearing at periphery of second whorl, developing some 16 low nodes (Figure 7); nodes disappearing on later whorls; minute axial threads continuing on surface of shell through last whorl, becoming stronger on siphonal canal. Spiral sculpture subtly developing at beginning of first whorl, approximately 8 strong threads showing on second whorl, 5 threads on shoulder, which will become strong cords on later whorls; three threads below periphery

disappearing on later whorls; spiral threads on early whorls creating a somewhat reticulate sculpture as they cross axial elements; two adapical threads strongest, wrinkled by axial elements. Siphonal canal straight or rather sinuous, long, approximately 30 to 35% of shell length. Aperture widely oval, with many faint interior lirae best detected by rubbing a fingernail or pin across the surface; width approximately 20% of shell length. Parietal wall smooth, without callus; columella with two strong, oblique anterior plications, posterior one somewhat bifurcate; plications inconspicuously continuing as two or three long axial elements in different degrees of strength along dorsal side of siphonal canal (Figure 5). Outer lip thin, with 5 denticles at posterior end reflecting terminations of pre-sutural cords. Shell color off-white with uneven penciled-like brown spiral lines that terminate at beginning of siphonal canal and that show through to inside aperture; columellar area and siphonal canal light tan, canal with sporadic dark brown blotches in mature specimens.

Type Material: Holotype (Figures 1–2), ANSP 450737, 277 × 105 mm, north of Cayos de San Andrés, Caribbean Sea, Colombia, trawled, 350 m,; paratype 1, ANSP 466083 (Figure 3), 182 mm, with operculum; Paratype 2, EFG 31404 (Figures 4–6), 170.1 mm,. All from type locality.

Other Material Examined: Two shells, LC unnumbered, 177.4 and 188.1 mm, trawled north of Cayos de San Andrés, Colombia, depth 350 m; one shell, LC unnumbered, 87.1 mm, Golfo de Morrosquillo, Colombia.

Type Locality: North of Cayos de San Andrés, Caribbean Sea, Colombia, 350 m.

Distribution: North of Cayos de San Andrés, Caribbean Sea, Colombia, trawled, 350 m; Golfo de Morrosquillo(?).

Etymology: From the Latin adjective *delicatus, -a, -um*, meaning delicate; used in the superlative to denote the unusual lightness and fragile nature of the shell.

Discussion: *Fasciolaria delicatissima* new species can be differentiated from most congeners by its unusually thin walls, its color markings and its paucispiral protoconch. The new species has been confused with *F. tephrina* de Souza, 2002 (Figures 10–13), and *F. cf. tephrina* (Figures 8–19, 14–16). *Fasciolaria delicatissima* shares with *F. tephrina* the large, capacious shell, the paucispiral protoconch, the deep-water habitat and relative geographic proximity. However, *F. tephrina* has a protoconch that deviates from the main axis, whereas the new species lacks that character; its protoconch is differently shaped, with a less convex first half of the whorl and a more bulbous second half (compare Figure 7 with Figures 9, 12 and 16). This difference is possibly what causes the protoconch of *F. tephrina* to be "deviated."

Early teleoconch whorls of *F. delicatissima* are differently sculptured, with more spiral elements and more numerous (16 vs. 10), weaker axial elements than those of *F. tephrina* (compare Figure 7 with Figures 9, 12,
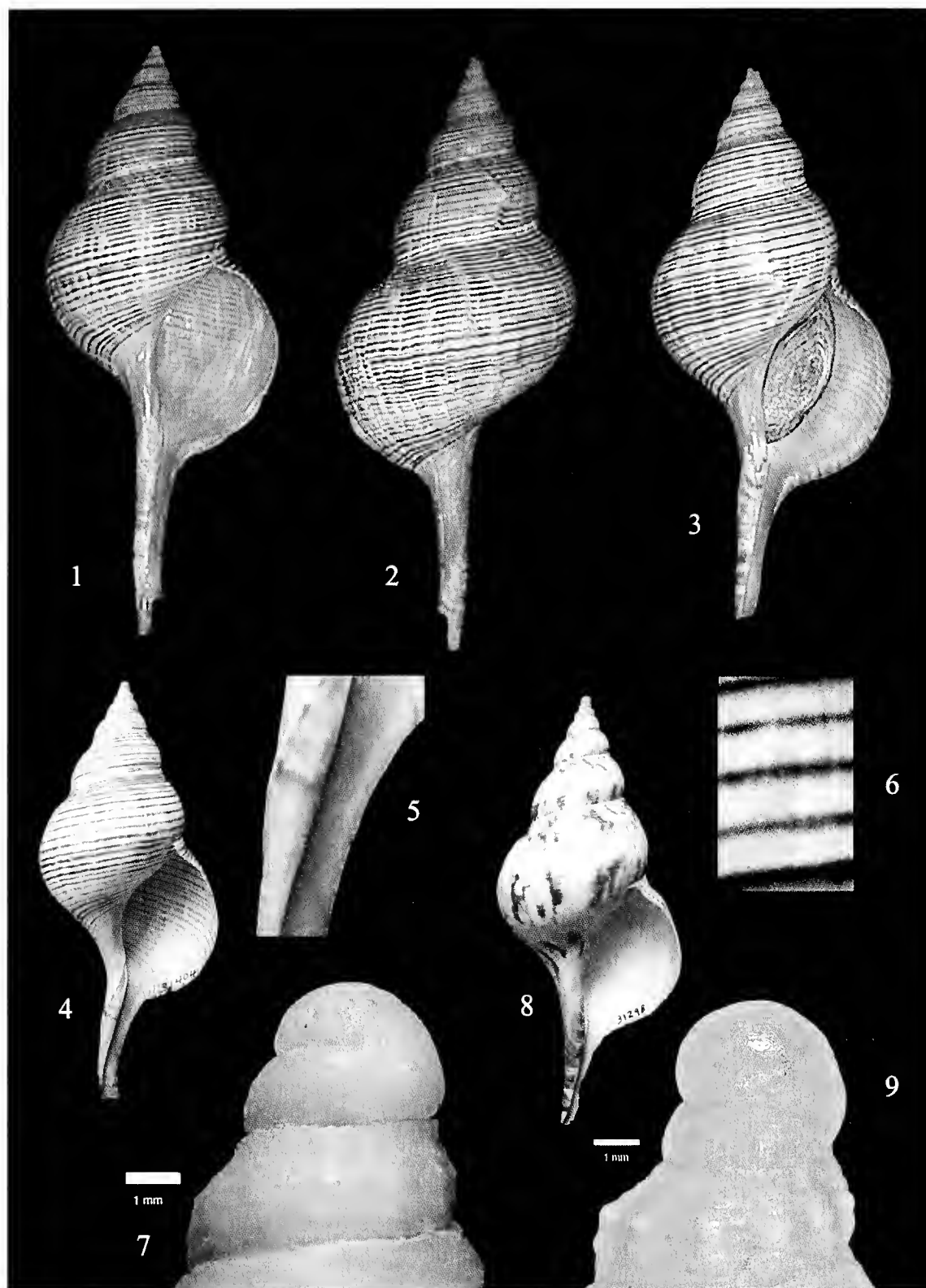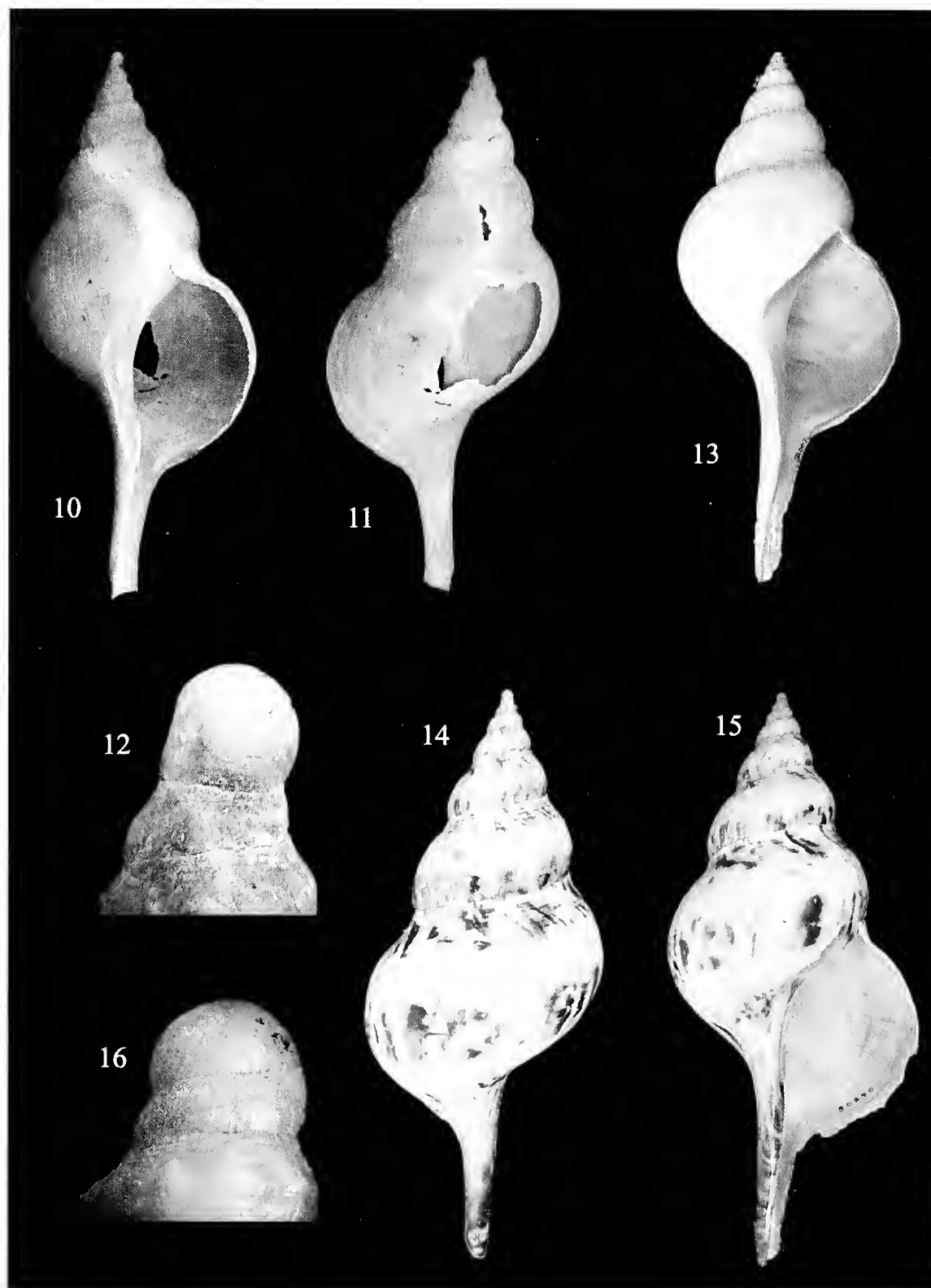
Figures 1–9. *Fasciolaria* species. **1–7.** *Fasciolaria delicatissima* new species, north of Cayos de San Andrés, 350 m. **1–2.** Holotype, ANSP 450737 (image copyright from Femorale with permission), length 277 mm, width 105 mm. **3.** Paratype ANSP 466083 (image copyright from Femorale with permission), 182 mm, specimen with operculum. **4–7.** Paratype, EFG 31404, length 164.9 mm, width 64.5 mm. **8–9.** *Fasciolaria cf. tephrina*, EFG 31298, length 165.9 mm, width 45 mm, near Honduras-Nicaragua border, in fish trap, 300 m.

and 16). Moreover, the shell surface of the new species is covered with minute axial threads evident under low magnification (Figure 6), its parietal area lacks an enameled wall, and the lirae inside its aperture are determined by tact; they are visually undetected. The two plications of *F. tephrina* are limited to the columella, but those

of *F. delicatissima* continue as ridges over the siphonal canal (Figure 5).

The shell of *F. delicatissima* is much thinner than that of *F. tephrina*. A 165.9 mm specimen of *F. cf. tephrina* (EFG 31298; Figures 8–9) weighs 46.06 grams, whereas a similar 164.9 mm specimen of *F. delicatissima*

Figures 10–16. *Fasciolaria* species. **10–13.** *Fasciolaria tephrina* de Souza, 2002. **10–12.** Holotype MZSP 35048, length 187.4 mm, width 73.8 mm, north of Quita Sueño Bank, 14°40′ N, 81°25′ W, in 480 m. **13.** EFG 31107, length 220 mm, width 85 mm, near Honduras-Nicaragua border, in fish trap, 300 m. **14–16.** *Fasciolaria cf. tephrina*, EFG 30890, length 230 mm, width 90 mm, near Honduras-Nicaragua border, in fish trap, 300 m.

(Paratype 2, EFG 31404, Figures 4–7) weighs only 23.16 grams.

The multilineate pattern and coloration of the shell of *F. delicatissima* is consistent in all specimens examined, differing from the white of *F. tephrina* (Figures 10–13) and the blotched pattern *F. cf. tephrina* (Figures 8–9, 14–16). The six specimens of *F. cf. tephrina* that were studied, all collected empty, clearly show the character-

istic blotched markings. Even the most eroded specimens have darker brown coloration at the tip of the anterior canal.

Although color intergrades between *F. tephrina* and *F. cf. tephrina* have not been seen, no differences between them are evident except coloration and a stronger enameled parietal shield in the white form. One may theorize that because all specimens of *F. tephrina* have been
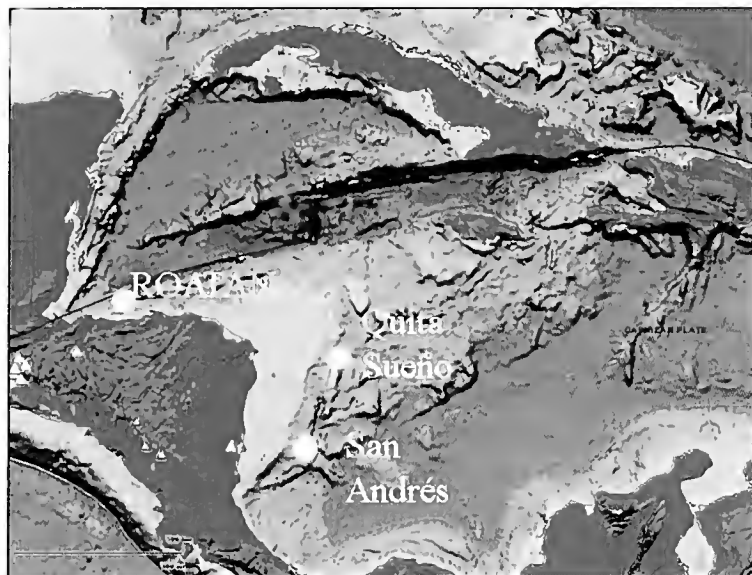
Figure 17. Bathymetric chart of the seafloor off Honduras and Nicaragua.

collected empty and the type material is in poor condition, shells of the white form could represent bleached material. However, several better-preserved specimens of the white form have come to light since the original description (e.g.,Yidi and Sarmiento, 2011, Figure 493; also Figure 13, herein) and they show no indications of coloration.

The bathymetry at the eastern edge of the Honduran continental shelf and slope is rugged and complex (Figure 17). Quita Sueño Bank is not far from the edge of the continental shelf, but the abrupt benthic topography between them may lend itself to the development of small allopatric populations, particularly with direct developers such as species of *Fasciolaria*. Fishermen may spend weeks at sea and obtain shells from several non-contiguous populations and as they range over the continental slope, but such bycatch may be landed in a single box, making precise origins of the shells difficult to ascertain.

We question the "Golfo de Morrosquillo" locality for *F. delicatissima*. The Golfo is much too shallow to support the species, which otherwise has not been reported despite intensive trawling for shrimp there for at least four decades. Data available for all of the other *F. delicatissima* specimens indicate that they were obtained by trawls; at least one specimen was collected alive (Figure 3), which confirms the efficacy of that collecting method. This implies that the species lives on a flat bottom accessible to trawlers, and that would be at the base of the escarpment (Figure 17). Conversely, *Fasciolaria tephrina* and *F. cf. tephrina* have been collected exclusively "crabbed" in fish traps, the seafloor not being conducive to trawling. The latter two forms do not

seem to intergrade, but until more precise catch data become available, they should be regarded as belonging to a single species.

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Research Note

A tumbling snail (Gastropoda: Vetigastropoda: Margaritidae)

In August 2015, the NOAA ship OKEANOS EXPLORER conducted deep-sea studies in the northwestern Hawaiian Islands, which now are within the Papahanaumokuakea Marine National Monument. The ship deployed the remotely operated vehicle DEEP DISCOVERER (D2 ROV), whose live video feed was shared with researchers on shore via satellite transmission.

On 5 August 2015, the D2 ROV was exploring angular basalt blocks and sediment patches on the steep inner slope of Maro Crater, an unusual 6 km-wide crater east of Maro Reef (25.16° N, 169.88° W, 2998–3027 m). The cameras recorded what appeared to be a fish attacking or being attacked by some other unidentified animal. When the ROV cameras were zoomed in on the encounter, the twisting elongate structure though to be a fish was determined to actually be the elongate foot of a gastropod mollusk (Figures 1, 2). No potential predator or prey could be seen in subsequent view, so it seems likely that the snail reacted to the close presence of the ROV. The mollusk first moved horizontally before falling down, retracting the foot and resting among the rocks. The camera was equipped with red strobe lights that set a scale of 10 cm. Because the camera's focal length changed, it is difficult to estimate how far the snail moved but 3 m seems to be a reasonable guess.

Examination of the shell of the mollusk (Figure 3) showed that it belonged to the genus *Gaza* Watson, 1879. Species of *Gaza* are among the larger gastropods to be found on the continental shelf and upper slope. They can be recognized by their size (to 40 mm), ivory color with a golden sheen, deep umbilicus, uncalcified operculum, and lack of a noticeable periostracum. Most specimens have been obtained by trawls on mud bottoms.

The mollusk recorded by the D2 ROV was not collected for verification. *Gaza daedala* Watson, 1879 is the only species of this genus known from the central or western Pacific. The only report for which a specimen is known is that of the holotype, collected at 19° 10′ S, 178°10′ E (off Kandavu, Fiji), 1100 m. Robert Moffett and Christopher Kelley (pers. comm.) informed me that a specimen of *G. daedala* was collected off Kauhuoa Point, Big Island of Hawaii (19.34° N, 155.91° W, 600–803 m, 24 August 1988, submersible vehicle PISCES,) but the specimen has been lost. Severns (2011) reported *G. daedala* from 330 m off Oahu but the material on which that report was based also is missing. The mollusk in the photographs has an iridescent shell with radiating lines, as reported for *G. daedala* (Simone and Cunha, 2006).

The width of the shell, based on the camera's scale dots, seems to have been close to 40 mm, with the extended foot as much as 100 mm. The characteristic covered umbilicus can only partially be seen in the photograph, so the identification remains uncertain. Hickman (2012) noted that species of *Gaza* from the Gulf of Mexico might be associated with chemosynthetic communities, but the mollusk in the photographs was living on manganese-encrusted basalt.

Hickman (2003; 2007) reported "foot thrashing" as an escape response to predators and in the laboratory by "mechanical disturbance" in the trochoidean gastropods *Umbonium vestiarium* (Linnaeus, 1758), *Isanda coronata* A. Adams, 1854, and other species of the family Solariellidae. The observations provided here are the first of such behavior in *Gaza* spp. and among the few reports on behavior of non-cephalopod deep-sea mollusks.

Supporting material: video is posted at http://oceanexplorer.noaa.gov/okeanos/explorations/ex1504/logs/dive4/dive4.html.

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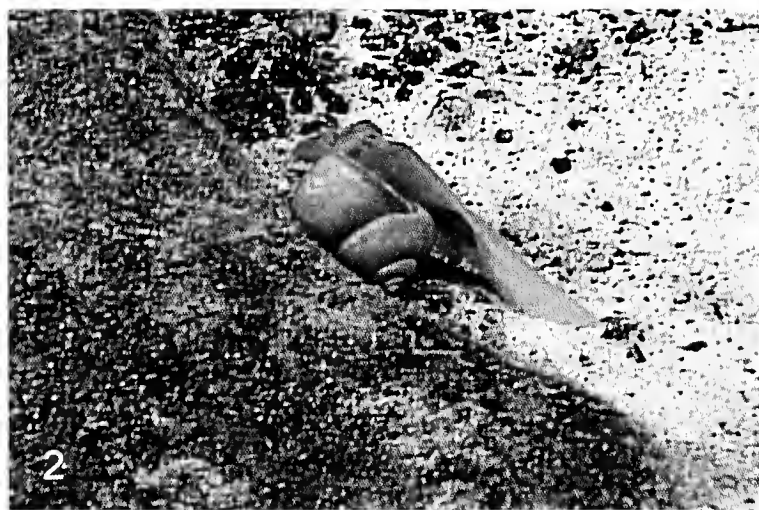
Figures 1–3. *Gaza sp.* **1, 2.** Individual tumbling with foot extended. **3.** Close-up detail. Photos courtesy of NOAA Office of Ocean Exploration and Research, 2015 Hohonu Moana Expedition.

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Research Note

The authorship of *Turrilatirus craticulatus* (Gastropoda: Fasciolariidae: Peristerniinae)

The specific name of the Indo-West Pacific gastropod *Turrilatirus craticulatus* generally has been attributed to Linnaeus, 1758 in the original combination *Murex craticulatus*, but the correct attribution is to Gmelin, 1791, in the combination *Voluta craticulata*.

In the tenth edition of *Systema naturae*, Linnaeus (1758: 755, sp. 495) introduced *Murex craticulatus* without reference to a figure or designated locality. Linné (1767: 1224–1225, sp. 569) repeated the description, added a phrase "*Turbo angulatus*," cited a figure by Rondelet (1555: 89) and added the locality "*M. Mediterraneo.*" Rondelet's figure shows a shell with about four angular spire whorls plus a body whorl and a relatively long siphonal canal.

Born (1778; 1780) and Chemnitz (1780) treated a different shell as *M. craticulatus*. Born (1780) and Chemnitz (1780) each re-described what they believed to be *M. craticulatus* Linnaeus and provided new figures, still accepting its Mediterranean locality. Richardson et al. (1979: 165) noted that Chemnitz figs 1382 and 1383 were cited by Born both in 1778 and 1780. That incongruity of dates was explained by Kohn (1964: 153), who provided evidence that Born received plates from Martini at least two years before they were published by Chemnitz. Chemnitz expressed uncertainty regarding the name, concluding that although the original description did not fit exactly, Linnaeus had intended it for a shell that Chemnitz recognized. The shell they described and figured, now well-known as an Indo-West Pacific species, is not the species that Rondelet figured, nor is it the one that Linnaeus described.

Gmelin (1791: 3554, sp. 105) repeated the Linnaean description of the Mediterranean *M. craticulatus*, again citing the Rondelet figure. Some pages earlier, however (1791: 3464), he provided a separate account for a new species, *Voluta craticulata*. The impetus for classification in *Voluta* apparently traces to Schröter (1783: 284), who cited "Martini iv [Chemnitz, 1780] tab. 1382 & 1383; Lister, [1688] Hist. Conch. pl. 919. fig. 13. mala. pl. 967, fig. 22; Seba [1758], pl. 50, figs 55 & 56, pl. 51, figs 31 & 32; Knorr [1764], pl. 3, fig. 6" in a taxon he called *Voluta* sp. Chemnitz had assigned these figures to *M. craticulatus* Linnaeus, but Gmelin cited all of them for *V. craticulata*. By these actions, Gmelin recognized that the species described by Linnaeus was not the shell figured by Chemnitz and Born.

From the start, Gmelin's distinction was misunderstood. Schreibers (1793: 121, 229) treated *M. craticulatus* and *V. craticulata*, citing correct figures for the latter but attributing both names to Linnaeus. Röding (1798) asso-

ciated *M. craticulatus* (not *V. craticulata*) "Gmel." with the Chemnitz figures and reclassified the species in *Fusus*. Dillwyn (1817) retained *M. craticulatus* Linnaeus but added *V. craticulata* Gmelin as a synonym. Lamarck (1822) placed *craticulatus* "Lin. Gmel. p. 3554" in *Turbinella* and cited "*Voluta craticulata* Gmel. p. 3464" as a junior synonym, as did Deshayes (1832), who cited the same figures cited by Gmelin. The species was maintained as *T. craticulata* by Schubert and Wagner (1829) and Kiener (1840), both of whom attributed the name to Lamarck as first user of the combination, and by Anton (1838) and Reeve (1847), who attributed the name to Linnaeus.

Deshayes (1843: 386) headed an account "*Turbinella craticulata* Lamk." but made clear in synonymy and in a footnote that the name's author was Linnaeus. Deshayes (1843: 457) later suggested that some characters mentioned in the brief original description of *Murex craticulatus* seemed to fit a variety of the Mediterranean species *Fusus syracusanus* (Linnaeus, 1758). This comment appeared in a footnote wherein Deshayes considered but did not accept the Linnaean name as an earlier name for *Fusus strigosus* Lamarck, now *Fusinus rostratus* (Olivi, 1792). Clearly, Deshayes was uncertain about the identity of the Linnaean name.

In another footnote, Deshayes (1843: 386) noted: "Sous ce nom de *craticulata* MM. Schubert et Wagner ont décrit et figuré une espèce très distincte du véritable *Murex craticulatus* de Linné et des autres auteurs." Similarly, Dodge (1957: 188) noted that Schubert and Wagner (1829: 103) had followed Lamarck's (1822) synonymy for *Turbinella craticulata*, but their figures showed an entirely different shell that he could not identify. Both Deshayes and Dodge overlooked the fact that the figures were for *T. craticulata* Lamarck "var. b" of Schubert and Wagner (1829: pl. 227, figs 4023 & 4024), which Anton (1838) later renamed *T. wagneri*.

Küster *in* Küster and Kobelt (1844: 21) cited for *T. craticulata* both *M. craticulatus* Gmel. Lin. p. 3554 and *V. craticulata* Gmelin p. 3464 but also cited for it the figures by Lister, Seba, Knorr, and Chemnitz (but not Rondelet), and attributed authorship to Gmelin.

Hanley (1855) remarked that the shell figured by Kiener (1840) (*i.e.*, the Indo-West Pacific *craticulatus*) "answers very correctly to the description by Linnaeus," but he soon changed his mind. Hanley (1856: 134) specified that *M. craticulatus* of Wood (1828), the *T. craticulata* of Kiener and others, was based on *V. craticulata* Gmelin, indicating his belief that the name applied to a different species.

Kobelt (1876a: 22) also attributed the name to Gmelin but mistakenly cited for it p. 3554, Gmelin's page for *M. craticulatus* Linnaeus. Kobelt (1876b: 54) mistakenly cited "*craticulatus* Lam." (*non* Linnaeus) as a junior

synonym of *Latirus turritus* (Gmelin, 1791), another Indo-Pacific species of *Turrilatirus* Vermeij and Snyder, 2006. Kobelt in Küster and Kobelt (1876: 118; 1877: 58) attributed *T. craticulata* to Gmelin, without mention of Linnaeus.

Tryon (1880: p. 93, pl. 69, fig. 159) identified *Latirus craticulatus* (Linnaeus, 1758) as the Recent Indo-West Pacific species. Tryon's assignment was unanimously followed until Dodge (1957) reviewed the Linnaean name. Dodge agreed that *M. craticulatus* Linnaeus and *V. craticulata* Gmelin applied to separate species, but he said that attribution of the name *craticulatus* Linnaeus to the Indo-West Pacific species had been so consistently accepted that it would be confusing to change it. Nevertheless, he recommended that, for a sound nomenclature, the Linnaean name should be regarded as a *nomen dubium*. On this we concur.

Dodge thought it difficult to disregard Gmelin's considerable synonymy but maintained that Gmelin only increased the confusion begun by Linnaeus because the description of *V. craticulata* is "equivocal," the shell size given by Gmelin is "somewhat too long," and no locality is given. Consequently, he advocated that Gmelin's name be ignored and *craticulatus* auct. be attributed to Dillwyn (1817), who had provided a new description for *M. craticulatus* 'Linnaeus' and cited the above mentioned appropriate figures. Nevertheless, all mentions of the Indo-Pacific species published since Dodge have ignored his recommendations. Most recently, Marais and Kilburn (2010: 128) correctly cited the original combination for the species as *V. craticulata* but attributed the name to Linnaeus.

No evidence supports the association of the Linnaean descriptions, the figure he cited, or the Mediterranean locality with the Indo-West Pacific species. There is no specimen of *Murex craticulatus* in the Linnaean collection (Hanley, 1855), nor was the species contained in the *Museum Ulricae* (Dodge, 1957), so no type material is available.

The remedy that Dodge proposed is impractical. Dillwyn's description and figures he cited may have been appropriate but he, like Born, presented the species as *M. craticulatus* Linnaeus, with Gmelin's name as a synonym, so Dillwyn's *M. craticulatus* is a junior primary homonym of the Linnaean name (ICZN, 1999: 59; Article 57.2), as are those of Born, Chemnitz, etc. The Chemnitz name is also unavailable as it was published in a rejected work (ICZN, 1987: 319). Conversely, Gmelin distinguished *V. craticulata* from *M. craticulatus* Linnaeus by providing separate accounts in different genera for the two species, by providing a separate description for the new species, and by citing figures wherein its identity is unmistakable. Clearly, the first available name for the Indo-West Pacific species is *Voluta craticulata* Gmelin, 1791.

For a discussion of the complex synonymic history of *Murex craticulatus* "Linnaeus" Brocchi, 1814, a Mediterranean muricid, see Houart (2001: 82–84).

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